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Prof. Agassiz,  
Member of the Institut 'Fr.

ANATOMY

from his friend

The Author.

OF

THE KING CRAB

(*Limulus polyphemus*, LATR.).

BY

RICHARD OWEN, C.B., F.R.S.

LONDON:

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1873.





TO  
THOMAS BELL, F.R.S. &c. &c.

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This Work, a development of a paper submitted, in fulfilment of his wish, to the Linnean Society, which prospered under his Presidency, and in which he continues to take the warmest interest, is affectionately inscribed by his old friend and fellow-labourer,

THE AUTHOR.

## CONTENTS.

|                                       | Page |
|---------------------------------------|------|
| § 1. Introduction .....               | 1    |
| § 2. External characters .....        | 3    |
| § 3. Muscular System .....            | 10   |
| § 4. Nervous System .....             | 15   |
| § 5. Digestive System .....           | 21   |
| § 6. Sanguiferous System .....        | 23   |
| § 7. Respiratory System .....         | 26   |
| § 8. Reproduction of Parts .....      | 27   |
| § 9. Generative System .....          | 27   |
| § 10. Development .....               | 29   |
| § 11. Conclusion .....                | 38   |
| § 12. Description of the Plates ..... | 46   |



ON  
THE KING CRAB

(*Limulus polyphemus*, LATR.).

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§ I. *Introduction*.—The living representatives of extinct groups of animals have always had peculiar attractions for my scalpel, especially when the lost group was large and the dissectible representative rare and exceptional in character. Such, *e. g.*, was the Kivi\*, sole survivor of the race of Moas; such the *Protopterus* or *Lepidosiren*†, the living representative of extinct notochordal, protocercal, cycloganoid fishes of palæozoic seas; such the *Nautilus*, in like relation to the extinct fabricators of chambered and siphonated shells ‡; such also were *Terebratula*, *Lingula*, and *Discina* §, as representatives of the Brachiopoda, and *Euplectella*, the surviving type in oceanic depths of the fenestrate *Ventriculites*.

With reference to the singular and interesting palæozoic Crustacea known chiefly, if not exclusively, in 1840, as ‘Trilobites,’ I was for a time uncertain whether to take the rare Isopod *Serolis*, of which a specimen was procured for me for that purpose by my friend Charles Stokes, Esq., F.R.S., the discoverer of the ‘labium’ or lip-plate in Trilobites (*Asaphus platycephalus*)||, or to look for their grade and plan of internal structure in *Limulus*.

The authority of W. Sharpe Macleay, after the appearance of his famous “*Horæ Entomologicæ*,” weighed about that time heavily upon us. All who had studied the Trilobites up to 1843 were of opinion that they were malacostracous. Audouin led the way by affining them to the Isopoda ¶; and Macleay, in an Appendix to Murchison’s great work on the Silurian strata, assigned to Trilobites a position as a distinct Order between the Isopoda and Aspidophora, basing his views on the trilobed character of the segments in *Serolis* and *Bopyrus*, and the character of the eyes in *Cymothoa*, which “were large, sessile, and compound, as in Trilobites. Moreover *Cymothoa* and other Isopods,” he remarked, “rolled themselves into a ball,” as Trilobites have been found to do before they perished.

The first general fact or view which influenced my choice in this matter was the character of the Malacostraca, founded on the number of body-segments,—seven for

\* “On the Anatomy of the *Apteryx australis*,” Trans. of Zool. Soc. vols. ii. & iii. (1838).

† Trans. Linn. Soc. vol. xviii. 1839.

‡ ‘Memoir on the Pearly Nautilus (*Nautilus pompilius*),’ 1832.

§ “On the Anatomy of the Brachiopoda of Cuvier,” Trans. Zool. Soc. vol. i. (1835); also ‘On the Anatomy of *Terebratula* and *Lingula*,’ Monograph, published by the Palæontographical Society in vol. for 1854. (The subjects for the anatomy of *Discina*, Sow., were referred to the genus *Orbicula*.)

|| Trans. Geol. Soc. Lond., N. S. vol. i. pl. 27.

¶ “Recherches sur les Rapports Naturels qui existent entre les Trilobites et les Animaux Articulés,” Annales des Sciences Physiques de Bruxelles, tom. viii. (1821).



the thorax, seven for the abdomen, and, admitting the same number (as indicated by sense-organs and appendages), seven for the head,=total twenty-one. Now this character could not be predicated of the Entomostraca; some had more, some fewer segments. *Branchipus stagnalis*, for example, had eleven thoracic and nine abdominal segments, besides the head protected by its cephalic shield. In *Isaura*, in which this shield is also present and of great size, the number of thoracic and abdominal segments exceeded twenty-four.

Amongst the Trilobites the part of the body next the shield-shaped cephalic one shows eight segments in *Asaphus platycephalus*, eleven segments in *Phacops*, and from thirteen to fifteen in *Calymene*, besides an abdomen of eight segments. Then there were departures in Entomostraca from the Malacostracous numerical or segmental character by defect as well as by excess,—forms, like *Limulus*, *e. g.*, with less than twenty-one segments.

Moreover “the trilobed character of the segments in *Serolis* and *Bopyrus* is present also in *Limulus*, the segments of its body, markedly in the hinder division, presenting three elevations or lobes. The eyes, it is true, are large, sessile, and compound in *Cymothoa*; but so are the larger pair in *Limulus*, and more like those of the Trilobite than the eyes of any Isopods are; the larval Limuli, moreover, roll themselves into a ball”\*.

The value of the numerical character of the segments of the body in the question of the affinity of the Trilobites was pointed out by me in a lecture on Crustacea published the week after its delivery, April 27th, 1843 †.

Burmeister, whose excellent work on Trilobites appeared at Berlin in a later part of 1843 ‡, insisted, with equally original views, on the importance of this character; but, for his remark that “*Limulus* was still more widely removed from the Trilobites than the Isopods are” §, I could not see adequate grounds.

All this, however, is now of mere historical interest; and I fully concur with my experienced colleague, Henry Woodward, Esq., F.G.S., whose labours have shed so valuable a light on the affinities and homologies of the Crustacea other than those in which “the normal number of segments is twenty-one,” that “the conclusions of Prof. Agassiz and James Hall as to the close affinity existing between the Eurypterida and the Xiphosura are correct”||. Whether the extension of Dana’s group, Merostomata, as

\* Owen, ‘Lectures on the Comparative Anatomy and Physiology of the Invertebrate Animals,’ ed. 1855, p. 331.

† In the following terms:—“The distinction between the Entomostraca and Malacostraca in the number of the segments of the body is of the first importance in determining the affinities of the ancient extinct Crustacea called ‘Trilobites.’” ‘Lectures on the Comparative Anatomy and Physiology of the Invertebrate Animals,’ 8vo, 1843, p. 165.

‡ A translation of this work, with notes, by T. Bell & Ed. Forbes, was published by the Ray Society in 1846.

§ In this view, however, Burmeister received the support of Emmerich in Leonhard und Bronn’s Neues Jahrbuch, 1845, part i., translated in ‘Taylor’s Scientific Memoirs,’ vol. 4, part xiv. p. 253, August 1845. Emmerich defines the “Trilobites as a peculiar order, connecting Malacostraca with Entomostraca, but nearer the latter. They are related to the former by their calcareous crust-like shell, and by their not possessing simple eyes in conjunction with compound eyes. The Woodlice (Isopoda) have, of all Malacostraca, the greatest resemblance to Trilobites.”

|| ‘Monograph of the British Fossil Crustacea belonging to the order Merostomata,’ Part I., Palæontographical Society’s vol. for 1866, p. 9.



expanded by Mr. Woodward \*, may or may not meet with general acceptance, it is plain that *Limulus* has closer affinities with *Pterygotus* and other Eurypteroid Crustacea of palæozoic age than with the Tribolites. My aim, therefore, in finally selecting, in 1843, *Limulus* for anatomical research reflecting light on the organization of palæozoic Crustacea, is equally fulfilled by the subsequent discoveries of Agassiz †, M'Coy ‡, Hall §, Nieszkowski ||, Salter ¶, Huxley ¶, and Woodward \*\*, of extinct Crustacea of as high antiquity as the Tribolites, and more closely represented by *Limulus*. I doubt not therefore that the following illustrations of the structure of their lingering representative will be acceptable to Palæontologists as well as to Comparative Anatomists.

The contributions to the anatomy of *Limulus* previously made will be noticed in connexion with the sections to which they belong ††.

§ 2. *External Characters*.—My remarks on this head need be few, and bear mainly on the intelligibility of the anatomical details.

\* ‘Reports and Proceedings of the British Association, Edinburgh, August 1871.’ Mr. Woodward exemplifies his views by the following concise parallel:—

“Order MEROSTOMATA, Dana.

“Suborder EURYPTERIDA.

I.

“Suborder XIPHOSURA.

“Ex. *Pterygotus* (Fossil, extinct).

“Ex. *Limulus* (Fossil, and living).

- “1. Eyes sessile, compound.
2. Ocelli distinctly seen.
3. All the limbs serving as mouth-organs.
4. *Anterior* thoracic segments bearing branchiæ or reproductive organs.
5. Other segments destitute of any appendages.
6. Thoracic segments *unanchylosed*.
7. Abdominal segments *free and well-developed*.
8. Metastoma *large*.

- “1. Eyes sessile, compound.
2. Ocelli distinctly seen.
3. All the limbs serving as mouth-organs.
4. *All* the thoracic segments bearing branchiæ or reproductive organs.
5. Other segments destitute of any appendages.
6. Thoracic segments *anchylosed*.
7. Abdominal segments *anchylosed and rudimentary*.
8. Metastoma *rudimentary*.”

† ‘Monographie des Poissons Fossiles du Vieux Grès Rouge,’ &c. 4to, p. xix. 1844.

‡ ‘Contributions to British Palæontology,’ Cambridge, 8vo, 1849.

§ Prof. James Hall, LL.D. ‘Natural History of New York,’ part vi. Palæontology, vol. iii. 4to, 1859.

|| Archiv für die Naturkunde Liv-, Ehst- und Kurlands, erste Ser. vol. ii. 1859.

¶ “On some new Crustacea from the Uppermost Silurian Rocks” (Salter), “Observations on the Structure and Affinities of *Himantopterus*” (Huxley), Quart. Journ. Geol. Soc. Lond. vol. xii. 1856; “On the Anatomy and Affinities of *Pterygotus*” (Huxley & Salter, in Monograph 1, ‘Memoirs of the Geological Survey of the United Kingdom,’ 8vo, 1859).

\*\* “On *Eurypterus lanceolatus*,” Geol. Mag. vol. i. 1864. British Association Reports, 1864. Quart. Journ. of the Geol. Soc. Lond. vol. xxi. (1865).

†† Straus Dürkheim, in his ‘Anatomie Comparée des Arachnides,’ June 1829, pointed out some particulars of structure, the “sternum intérieur,” *e.g.*, in which *Limulus* resembled the spiders. This led Latreille to designate the *Limuli* “Crustacés-arachnides” (Dictionnaire d’Histoire Nat. Art. ‘Entomologie, *Limuli*’). Other resemblances to Arachnides in organization will be pointed out in the present memoir. Whence I infer that *Limulus* and the extinct members of the order Merostomata exemplify a more generalized condition of condyloped organization, from which the Arachnida, quitting the waters, may have diverged as a special branch of air-breathers.



The body of the American as of the Moluccan King-crab (*Limulus*) consists of three principal parts—two large, broad, depressed, and shield-shaped, as viewed from above (Pl. V A., B), the third long and spike-shaped (*ib.* c).

For the description of the external characters of these parts, which are not here noticed, I refer to the elementary works on Crustacea and to the undercited excellent treatise by Van der Hoeven\*.

The homologies propounded by the Dutch monographer have not, however, been generally accepted. "It is evident," he remarks, "that the foremost division ['premier bouclier'] answers to the head and thorax of insects; for the feet are attached thereto, whilst it bears on its upper surface the organs of vision. Thus the head is here confounded with the thorax, and we believe ourselves authorized to give to this first buckler the name of 'Cephalothorax,' which naturalists assign to the first part of the body of Arachnidans" †.

This homology seems not to have been so evident to subsequent crustaceologists. Milne-Edwards, Thos. Bell, Spence Bate, Prof. Dana, and, above all, those eminent observers, Salter, Huxley, Woodward, who have devoted themselves so laboriously and successfully to the study of the palæozoic Crustacea, to which *Limulus* is most closely allied, reject it. According to them, the 'cephalothorax,' V. der H., answers only to the 'head' of Insects and Crustaceans.

There is, of course, a corresponding discrepancy as to the homology of the second division of the body of *Limulus*. "Le second bouclier répond à l'abdomen des Arachnides," according to V. der Hoeven‡. It is the 'thorax' of the above-cited later carcinologists.

At this point I venture to submit the following remarks:—The first division (A in all the plates), which constitutes, in *Limulus*, the major part of the entire body, which includes, besides the mouth, the brain, and organs of sense, also the major part of the neural axis, the same proportion of the heart and of the genital organs, together with the stomach, liver, and half of the intestinal canal, has obvious analogies with both head and abdomen of higher animals. The second division (B in all the plates), which in both *Limulus* and *Scorpio* includes the lamellate respiratory organs, the continuation of the heart, of the intestine, and of the neural axis, with the terminal outlets of the genital organs, as obviously repeats characters of both thorax and abdomen of higher animals.

The so-termed 'cephalothorax' of Arachnology, which is, as Van der Hoeven rightly recognized, the homologue of the first division of the body of *Limulus*, does not include the segments and appendages answering to those called 'thoracic' in modern crustaceology. The 'abdomen' of *Scorpio* (Audouin) and of *Limulus* (Van der Hoeven) does correspond with the so-called 'thorax' of carcinologists.

To apply the terms 'cephalon,' 'caput,' or 'head,' to the division of the body of *Limulus*, above characterized, seems, however, to be an extension of the use of such term beyond fair and reasonable bounds.

\* Van der Hoeven, 'Recherches sur l'Histoire Naturelle et l'Anatomie des Limules,' fol. 1838. The species which he dissected was the rapier-tailed Molucca Crab (*Limulus rotundicauda*, Latr.).

† *ib.* p. 10.

‡ *Op. cit.* p. 11.

If like considerations have led careful and conscientious describers to propose definite terms, giving an escape from wrong analogies suggested by those borrowed from vertebrate nomenclature, for the various appendages of the exoskeleton of Crustacea\*, I venture to hope that the term 'cephaletron' may meet with some acceptance as applied to the anterior division of the body in both *Limulus* and *Arachnids*, and that the term 'thoracetreron' may have the same fortune in relation to the second division of the body. Both terms indicate the composite analogies with the three great divisions of the body in anatomy; neither of them indicates or infers an homology adverse to the general conclusions which the ablest students of recent and fossil Crustacea have arrived at and agreed upon.

The Greek term 'ἡτρον' signifies a part of the abdomen; and a part of such cavity is associated with the 'head' in the first division of the King-crab's body, and with the 'thorax' in the second division. For the third division (c in all the plates) I willingly adopt Mr. Spence Bate's proposed term of 'pleon,' including therein the part he calls 'telson,' the whole constituting the characteristic 'tail-spine' of the present singular genus.

For the six pairs of articulate limbs, or appendages, of the 'cephaletron' (Pl. II. fig. 2, II-VII), I accept the homologies, and consequently adopt the terms applied to them by Bell †, Woodward ‡, and others.

These appendages are interesting in the present ancient form of the crustaceous class through the small amount of differentiation to which they have been subject. The homologue of the 'antennules' or 'internal antennæ' (II in all the plates) of higher and later Crustacea, is a forcipated limb, differing by its less number of joints and smaller relative size from the succeeding forcipated pairs. It is interesting, also, to note that in *Scorpio*, which, like *Limulus*, goes back to the 'Coal-measures,' the corresponding 'antennules' are forcipated. In *Limulus*, however, the antennules are articulated by 'gomphosis' to the sides of the base of a small 'labrum,' which is wedge-shaped, with the edge below.

Another analogy to *Arachnida* is exemplified in the 'outer antenna' (III, *ib.*), or second pair of limbs of *Limulus*, inasmuch as it is the seat of a sexual character. In the male of *Limulus polyphemus* it is monodactyle, the last joint being in shape a slightly bent claw (Pl. IV. fig. 1, III). In the male *Limulus moluccanus* both second and third pairs of limbs are so modified §. In the females of both species the corresponding limbs are forcipated (Pl. II. fig. 2, III). In both sexes the limbs succeeding the first pair, besides the addition of two basal segments (*ib.* fig. 3, 1, 2), have a marked increase of length, and go on more gradually lengthening to the sixth (VII, *ib.*). This pair (Pl. II A. fig. 4) has an additional joint (*ib.* 7). A long, slender, bi-articulate appendage (*ib.* 7) is articulated to the outer end of the hind border of the transversely extended haunch (*ib.* 1).

\* As, e. g., "siagonopod," "pereiopod," "pleopod," "uropod," &c. proposed by C. Spence Bate in the 'History of British Sessile-eyed Crustacea,' part. i. p. 3 (October 1861).

† 'History of British Stalk-eyed Crustacea,' p. xx. (1853).

‡ 'Monograph on British Fossil Crustacea,' &c. 4to, 1866, p. 4.

§ Van der Hoeven, *ut supra*, pl. i. fig. 3.



The inner border of the haunch is denticulate (*ib. p*), but in a less degree than in the four preceding pairs: all are subservient to the preparation of the food for the mouth, which is surrounded by these carding bases of the cephalotral limbs. A subulate appendage (Pl. II A. fig. 4, *s*, & Pl. IV. fig. 1, VII. *s*) is attached to the inner angle of the distal end of the fourth joint of the sixth limb. The penultimate joint of the same limb, instead of supporting merely the opposing blade of the chela or pincer, has four petal-like appendages (*ib. e, t*), besides a minute, elongate, slender pincer (*ib. r, u*), terminating what seems to be the normal continuation of the limb-joints.

The arrangement of the six pairs of limbs, in relation to the mouth, is shown in Pl. II. fig. 2, in a female *Limulus polyphemus*. It is here seen, as in fig. 1, Pl. IV., that these limbs are aggregated in a limited tract of the concave ventral surface of the cephalotron (A), and are so small in proportion as to suggest their inability to perform more than an accessory share in the locomotion of the species. The last alone, or 'maxilliped' (VII), is modified for such function.

Behind this pair of limbs are attached a pair of compressed spinigerous oblong plates (Pl. II A. fig. 2\*, & IV. fig. 1\*), slightly divergent, with the spinous border directed downward or 'ventrad'; they recall to mind the pectinate appendages of the thoracetron in *Scorpio*. In *Limulus* they close or complete the oral armature posteriorly, form the 'lèvre inférieure' of Cuvier †, and a corresponding member of the 'trophi,' according to Savigny; but Latreille preferred to regard them as the haunches or jaw-lobes of the sixth pair of limbs detached‡. The haunch-joints, however, are present, though less dentated, in the limb VII. (Pl. II A. fig. 5, *i*); but their palpal part (*ib. p*) is supplied by nervules having origins distinct from those of the main limb-nerves. The appendages in question have also their own distinct pair of nerves (Pls. II A. & IV. fig. 1, *n\**), arising between the origins of the main nerve of the limb VII. and that of the ganglionic chord, suggestive of a serial homology with the palpal nervules. I am not, however, satisfied with this as a ground for regarding the parts in question as detached limb-palps; and I, therefore, propose to call them 'chilaria' §.

The dorsal surface of the cephalotron is moderately accentuated: certain longitudinal tracts are depressed or produced inwardly, to afford advantageous attachments to muscles; other tracts are elevated to support the eyes, as outlooks, and also bearing defensive spines.

The ocelli (*a* 1 in all the figures) are placed one on each side of the anterior elevation of the mid ridge, which is the highest point toward the fore part of the cephalotron, and from which the dorsal surface of that broad semilunar shield slopes rapidly down to the curved digging-edge. The larger compound eyes (A 1) are equally favourably placed for a lateral outlook, each upon the outer part of an elevation about the middle of the longitudinal lateral ridge, from which the dorsal surface also slopes rapidly to the digging-edge. The almost horizontal tract between the lateral ridges, bisected by the median ridge, is traversed by the two longitudinal depressions, which are rather nearer

† "La lèvre inférieure est en arrière de la dernière paire de mâchoires, et formée de deux lames dentelées." Tableau élémentaire de l'Histoire Naturelle des Animaux, p. 452 (8vo, 1797).

‡ Cuvier's 'Règne Animal,' ed. 1828, vol. iv.

§ Gr. χείλαριον, a small lip.



the median than the lateral ridges. These depressions, with the median and lateral elevations, give the trilobitic character to the carapace or dorsal wall of the cephalon of *Limulus*. Each longitudinal ridge terminates by a short spine posteriorly. They are much produced in the carboniferous Limuloids, *e. g.* *Prestwichia*, as in some Trilobites, whence they have received the name of 'genal,' or 'cheek'-spines (in *Trinucleus*, *e. g.*).

The hind vertical part or border of the dorsal wall of the cephalon is divided into a median transverse tract of equal extent with the fore border of the thorax there-with articulated, and two lateral oblique tracts passing outward and backward to the hinder angles of the cephalon, which are usually spiked (Pl. V, A''). The transverse posterior tract is vertically thick, as if truncate. At the middle third, included by the hind deepened ends of the lateral longitudinal dorsal furrows, the upper border rises like the slopes of a low roof on each side to the median longitudinal dorsal ridge, here raised into a spine. The border below this is arched for the reception of the fulcral levator-process of the thorax, which passes beneath the arch. The joints of the thorax with the cephalon are at the straight lateral tracts on each side the convex process, entering the arch and at a lower level. Consequently a power tending to protract or pull forward the process, being opposed by the joints or centres of motion below, raises the thorax upon those centres, and brings it to a line or to a level with the dorsal plane of the cephalon, or even raises it to a slight angle therewith. At the lower part of the transverse hinder tract, outside the piers of the arch, are the pair of small crescentic pilose depressions (Pl. I. fig. 1, *h*) corresponding with the origins of the entapophyses within. From the posterior spine (*ib.* *k*), terminating the lateral ridge of the dorsal surface of the cephalon, a lower ridge passes downward and outward, to be lost in the lateral tract of the hind border. The indentation or groove between the ridge and border is continued along the thick transverse hind part of the cephalon, defining the portion below, which articulates with the thorax. In this groove is situated the entapophysial pit (*h*). To the lower part of the so-defined hind surface of the cephalon is attached the opercular plate, or first coalesced pair of lamelliform limbs (Pls. II., fig. 1, IV., fig. 1, VIII). I view the groove above described as a persistent indication of an originally separate segment. This segment, by the entapophysial pits above and the lamelliform appendages below, belongs to the category of 'thoracetal' plates: it is cephalotral only by confluence.

The general aspect of the cephalon of *Limulus* reminds one of a rounded spade-blade, or the blade of a saddler's knife. It gives forward a digging-edge, curving outward and backward to nearly twice the breadth of the following segment; so that this can be drawn along in the track delved out by the foremost one with least resistance. The hard chitine (Pl. II A. fig. 2, *f*) of the arched upper surface of the cephalon (*b*) meets a flat tract of the same material below (*ib.* *c*), at an acute angle, to form the digging-edge (*d*); and this edge is strengthened by a low ridge, like the carpenter's 'bead,' running above it, along the extent where most resistance has to be overcome, the 'bead' subsiding or falling into the edge at the hinder angular spiked ends (Pls. I. and IV. A''), which terminate outside the thorax (*ib.* B), nearly halfway toward the hind end of that division of the body.

The flat under surface of the digging-blade (Pls. II., III. *c*) is broadest at the point of most resistance, viz. at the foremost part of the curved edge. From this part the flat tract extends backward to its hinder border, which forms a pair of bold curves, arching outward and backward from the hindmost point, which is in the mid line, and in the form of a retroverted spine, supported by a vertical buttress-like ridge. The under hard chitine (Pls. II., III. A') rises rapidly from the curved hind borders of the flat part of the blade toward the softer chitine, forming the arched or vaulted roof and sides of the cavity concealing the mouth and its environing pairs of jaw-feet as the crab is viewed from above. Into this vault will slip or be pressed the sand or mud displaced by the forward and downward thrusts of the spade; and the burrower will have the advantage of the additional firmness so given to the cephalotron as a point of resistance to the fulcrum and muscular powers then acting from it upon the thoracetron and the telson, drawing them in, and fixing the latter in the position in which, like an 'alpen-stock,' it can best help forward in the renewed locomotive act, when the muscular powers and entapophysial fulcrum combine their mechanism to again move forward and press down the great cephalotral spade.

Meanwhile, in the loosened mud or sand so driven back into and filling the under hollows or vaults, the six pairs of jointed circum-oral appendages are busily at work sifting the displaced material in quest of whatever organic matter may be included fit for food.

Save the groove extending along the posterior facet, all traces of the segmental constitution of the cephalotron are obliterated in its growth, and are recognizable, externally, only through the appendages and sense-organs of this main division of the body.

In the thoracetron the segments are indicated not only by the appendages beneath, but by the pairs of entapophysial pits above, and by the notches and their articulated spines on each side. These spines are the 'épines latérales' of Van der Hoeven\* (*m* 1-6, Pl. I. fig. 1); the fixed spinous productions (*ib.* *n*, *n*) of the borders of the alveoli of *m* 1-6 are termed by Van der Hoeven the 'teeth'†. The hindmost of this series (Pl. I. fig. 1, *n* 7) terminates the lateral border, and projects beyond the posterior concavity for the articulation of the tail-spine (*c*).

The trilobitic accentuation of the upper surface of *Limulus* is continued on to the thoracetron by the pair of longitudinal depressions beginning where those of the cephalotron end, and extending about halfway along the thoracetron: in these depressions are the series of narrow oblong pits, commencing with the pair (*ib.* *h*) in the coalesced segment at the back of the cephalotron, and which, as they indicate the places of attachment of the entapophyses projecting from the inner surface, I term 'entapophysial:' there are six in each series (*ib.* fig. 2, *i* 1-*i* 6) in the thoracetron proper, seven with those of the opercular segment, *h*. The intermediate rising is subangular, with a spine at the fore part of the ridge, a second at the part where the longitudinal depressions cease, and a third at the hind end of the

\* *Op. cit.* p. 11.

† "Nous donnerons le nom de *dents* aux épines immobiles, et nommerons simplement *épines latérales* celles qui sont articulées."—*Ib.* p. 11.



mid-rising. The lateral, low and broad, convex risings exterior to the depressions subside where those terminate rather more than halfway toward the hind border of the thoracetron.

The under surface (Pls. III. & IV. B') defines the cavity lodging the articulate lamelliform appendages by a prominent border, within which the chitine loses density, where it forms the roof of that cavity. To this roof, or to the ventral surface of the thoracetron, are attached five large articulate, externally ciliate, lamelliform appendages (IX-XIII in all the figures), each representing a pair, more or less confluent along the median line. The similarly shaped appendage (VIII in Pls. II A. and IV.) is usually regarded as the foremost of this series; it supports the genital outlets, which are situated on the dorsal surface of the basal confluent segments (Pl. IV. figs. 6 & 8, *p*). It consists of three joints, of which the third retains the primitive parial distinction, and supports a small appendage, or fourth joint (*ib.* fig. 6, *4*). On the outer or ventral surface two oblique lines mark off a small median portion of the third segment. On the inner or dorsal surface the genital outlets are seen at *p*, and the insertions of the levator muscles at *m* <sub>11</sub>: the articular surfaces at which this coalesced pair have been detached are marked *r*.

The succeeding thoracetrals appendages are 4-articulate, as is shown in the sections of IX-XIII in Pl. II. fig. 1. The basal joints are confluent medianly and ciliate laterally, like those of the first, they having attached to their upper or dorsal surface, along its outer two-thirds, the branchial lamellæ (Pl. V. fig. 2). The three distal joints preserve their median distinction: the last joint is narrow, ovate, and projects beyond the lateral divisions of the broader antecedent joint.

The first pair of confluent lamelliform appendages are commonly termed 'opercular,' as they cover the space into which the genital apertures emit the products from the inner or upper surface of such appendages. But each of the succeeding pairs are equally 'opercular,' inasmuch as they closely overlap each other, shutting in the gills: the marginal slits, defended by a fringe of cilia, allow the sea-water to filter through to the branchiæ, and exclude the particles of sand or mud diffused abundantly, by the rapid action of the cephalotral limbs, through the respiratory medium during the burrowing procedures.

The tail-spine ('pleon' and 'telson,' *c* in all the Plates) nearly equals in length the two antecedent divisions: it is three-sided, with one ridge or angle dorsal and two lateral, bounding the lower or ventral flattened or slightly excavated surface\*. The ridges are roughened with short retroverted spinules. The base of the tail has three prominences,—an upper fuleral one, which, in the extended state of the spine, fits into the arched fossa beneath the back border of the thoracetron: this process receives the insertions of the 'levator muscles.' The other two prominences form a pair of articular condyles, adapted to cavities completed below by a pair of prominences of the thoracetron, developed within the semicircular lower excavation, receiving the condylar part of the base of the tail-spine.

\* The grounds for inferring a confluence of 'pleonal' segments forming the basal part of the spine will be subsequently given.



The structure of the teguments in *Limulus polyphemus* agrees with that in *Limulus moluccanus* \*.

§ 3. *Muscular System*.—The parts sent inward from the crust or exoskeleton are those that afford attachment to muscles, and those which also form or contribute to the joints of the articulate appendages. They are termed ‘entapophyses’ and ‘apodemes.’ The ‘apodemes’ that relate to the cephalotrichal limbs (Pl. V. II–VI) are broader and more complex than those of the thoracetron (*ib.* VII–XIII). The most conspicuous entapophyses are the following:—A pair of oblong lamelliform processes descend from the segment confluent with and forming part of the hind border of the cephalotrichon at the parts indicated by the ciliate depressions (Pl. I. fig. 1, *h*). Six pairs of similar, but rather smaller, processes project into the cavity of the thoracetron, from the inner surface of the parts indicated by the oblong depressions (Pl. I. figs. 1 and 2, *i* 1–6). These serve to give attachment to and augment the force of muscles. Analogous entapophyses are developed in most of the articulations of the limbs (Pl. II A. fig. 3, *c*, *e*, *g*) for a like purpose. All these internal processes assume more or less of a cartilaginous character, losing the hardness and colour of the outer crust as they extend inwards.

The main movements of *Limulus* in locomotion are those of inflection and extension of the cephalotrichon upon the thoracetron, and of the tail-spine upon the latter, and reciprocally.

The fixed points from which cephalotrichal muscles act upon the thoracetron are afforded not only by the apodemata and entapophyses, but also by the representative of an internal skeleton. This (Pl. II A. figs. 1 and 2, *h*) is situated partly in the angle between the gullet and stomach, thence extending backward a short way along the interval between the beginning of the intestine and the neural axis. It is an oblong sub-quadrate plate of sclerous or fibro-cartilaginous tissue, and is chiefly related to the attachment of muscles (Pl. IV. fig. 5). It was likened by its discoverer, STRAUS DÜRRCKHEIM, to an internal cartilaginous sternum, and may answer to the part which he so terms in *Arachnida*. I shall refer to it, without any wider homological signification, as the ‘entosternon.’

*Levatores thoracetri*.—The extensors or, more properly, ‘levators’ of the thoracetron are a pair of powerful muscles, the fibres of which rise from the low inner ridges indicated or formed by the longitudinal medilateral grooves or inflections of the carapace †. This feature in the accentuation of the upper crust of the cephalotrichon relates to such favourable condition of origin of the ‘levatores thoracetri.’ The pair come into contact at the median line, filling the hollow of the roof, of which that line is the mid ridge: their longitudinal fibres (Pl. II A. fig. 1, *m* 1) intervene between it and the pericardium, as they pass backward to be inserted into the anterior and upper transversely convex process of the thoracetron, *g*, which enters the corresponding arch, *f*, of the cephalotrichon.

*Depressores thoracetri*.—The flexors or ‘depressors’ of the thoracetron rise from the

\* Van der Hoeven, *ut supra*, p. 15.

† The corresponding grooves rendering *Asaphus* &c. ‘trilobitic’ most probably indicate analogous ridges or entapophyses for the flexor muscles of the segments.

dorsal surface of the hinder third of the entosternum (Pl. IV. fig. 5, *m*<sub>2</sub>), divide as they pass backward into two groups, or a pair, the fibres of which ascend obliquely on each side the intestine, and subdivide into fasciculi (Pl. I. fig. 1, *t*, *t*), to be inserted into the entapophyses of the thoracetrone.

*Prætrahentes entosterni*.—The power of the ‘entosternon’ as a fixed point or fulcrum is provided for by other muscles. A strong longitudinal subdepressed fasciculus rises from the inner surface of the fore part of the cephalotrone on each side, the fibres of which slightly converge as they pass backward to be inserted into the anterior angles of the entosternon (Pl. IV. fig. 5, *m*<sub>3</sub>)\*. They tend to draw that part forward, and resist the backward displacement of it, which would otherwise ensue in the action of the ‘depressores thoracetri’ (*m*<sub>2</sub>). The ‘prætrahentes entosterni’ are the main origins or ‘fixed points,’ functionally, of the great muscles, made ‘digastric’ by the intervention of the entosternal fibro-cartilage, which depress the thoracetrone: when the insertional lamellæ of the ‘depressores thoracetri’ become fixed points, they act through the medium of the entosternon as origins of the digastric muscles deflecting the cephalotrone. In like manner, when the insertions of the ‘levatores thoracetri’ become the fixed points or origins, those muscles will oppose the ‘depressores cephaletri,’ and become ‘levatores’ of that part.

*Levatores antici sterni*.—But the singular structure which acts functionally as ‘endoskeleton’ in *Limulus* has additional powers given to it by muscles which, like the mainstays of a mast, steady it in the transverse or lateral directions. From near the fore part of the dorsal surface of the entosternon diverge a pair of sclerous processes, which become tendons of a pair of muscles (Pl. IV. fig. 5, *m*<sub>4</sub>)†, about half the size of the ‘protractores’ (*ib.* fig. 5, *m*<sub>3</sub>) and which have their fixed points in the antero-lateral parts of the cephalotrone. The ‘levatores,’ by their direction, tend to raise and draw forward the entosternon, and so add their power to the protractors when these muscles are made to act in combination with the ‘depressores thoracetri;’ but to the degree in which their oblique course would tend, if one of the pair acted singly, to pull the entosternon sideways, their combined action would add to its fulcral power in relation to the movements of the two chief divisions of the body.

*Levatores laterales entosterni*.—The steadying of the entosternon is more directly attained by a series of fibres which, rising from the ridges due to the inflection of the lateral longitudinal grooves of the cephalotrone, descend and converge to be inserted into the posterior half of the lateral borders of the entosternon (*ib.* *m*<sub>5</sub>).

*Levatores postici entosterni*.—Fasciculi from the dorsal surface (Pl. IV. fig. 5, *m*<sub>6</sub>), which seem to be the fore part of the series of ‘depressores thoracetri,’ ascend, as they retrograde, to be inserted into the lamelliform entapophyses rising from the hind border of the cephalotrone, which seem to initiate anteriorly the series of shorter and smaller ones descending from the thoracetrone. With the insertion, or rather origin, of the above entosternal muscles, their action would be to retract and raise the entosternon.

The functions of these ‘levatores entosterni,’ in relation to the fixation of the endo-

\* Van der Hoeven, *op. cit.* p. 47, pl. iii. fig. 7, *a*.

† *Ibid.* fig. 7.



skeleton, are more especially in opposition to muscles arising from its lower and lateral parts to be inserted into basal entapophyses of the five posterior pairs of cephalotral limbs. But the principal muscles acting on the basal joints of these members arise from the 'apodemata,' or inflexions of the ventral crust (Pl. V. fig. 1, II-VI), forming, or rising from, the articular cavities in the cephalotral plastron for those limb-segments\*.

The '*levatores telsi*' (Pl. I. fig. 2, *u, u*), if I may be permitted to latinize Spence Bate's term for the 'tail-spine,' rise from the upper median lateral parts of the inner surface of the thoracetron; the median fasciculi form one elongated muscle (Pl. II A. fig. 1, *m 7*), which is inserted into the upper basal process, and directly tends to raise the spine: there are two shorter lateral masses (*ib. m 8*) converging to be inserted into the same process, but which, if acting independently, would draw the spine outward as well as upward. Both median and lateral muscles acting together would raise the spine forcibly, or if the spine were the fixed point, and the thoracetron depressed at an angle therewith, would tend to raise that part.

*Depressores telsi*.—Two shorter and broader but powerful muscles (*ib. m 9*), having the double oblique or penniform disposition of fibres, rise from the lower terminal part or segment of the thoracetron (*ib.*), and converge to be inserted into the sides of the basal entapophyses from below the articular condyles of the tail-spine. These, combining in action, depress the tail-spine; their lateral portion, combining with the corresponding one of the levator telsi, draws the spine to that side. When the spine was fixed the muscles would act as flexors, extensors, or abductors of the thoracetron.

Muscular fasciculi for the protraction and retraction of the thoracetratal appendages rise from the apodemata of that division of the body.

*Protractores branchipedum*.—The limb-plates of each lateral moiety of the broad gill-bearing lamella has two principal muscles: one, arising from the outer part of the apodeme in advance, subdivides into fasciculi, which descend, penetrating the fore or under surface of the gill-limb (Pl. II A. fig 1, *m 10*), and radiate therein to be attached to the several segments. These fibres protract the limb, change its recumbent for the erect position, and in that movement separate the gill-plates and facilitate the flow of water through their interspaces.

*Retractores branchipedum*.—These muscles rise from the base of the apodeme of their own gill-foot, near the place of articulation of the latter, and spread upon the hinder, inner, or upper surface of the proximal lamelliform joint before penetrating the interior of the succeeding ones. They retract or draw up the gill-feet, approximate and press together the gill-plates, and squeeze out the water from their interspaces. The insertional fibres of this muscle are shown on the anterior thoracetratal lamelliform limb, which serves as a cover or 'operculum' to the genital outlets (Pl. IV. fig. 6, *m 11*).

Some small fasciculi, combining their insertions with the proper muscles of the branchipeds, have attachments to the thoracetratal entapophyses, and seem to combine a levator action upon the branchipeds with that of the '*depressores thoracetri*.'

In the cephalotral limbs (III-VI, Pls. II. and III.) the haunch-joint (*coxa, 1*) is of great

\* Van der Hoeven, *op. cit.* pl. iii. fig. 10, *b, c*.



transverse extent, and besides affording insertion to the apodemal muscles, which forcibly work the carding-plate, or 'palpus' (Pl. II A. figs. 2-5, *p*), gives origin to muscles acting on the second joint or 'basis' (*ib. ib. 2*).

*Extensor basis pedis*.—One of these, of small size, is an extensor of the 'basis' (Pl. II A. fig. 5, *a*), but only in a slight degree.

The '*flexor basis*' (*ib. b*) is a larger, especially broader, muscle, and bends the 'basis' forcibly upon the 'coxa' or first joint.

*Flexor merii cnemique*.—The muscle (*ib. d*) arising from the 'basis' (2) is supplemented by other fibres from the 'merion,' or third joint (3), proceeding penniform-wise to an entapophysis, *c*, attached to the base of the 'cnemion,' or fourth joint (4). The action of this series of fibres is to bend both merion and cnemion. An 'extensor of the cnemion' is feebly developed.

*Flexor propedis*.—The cavity of the cnemion is chiefly occupied by the penniform flexor, *f*, of the 'propes' (5), upon which it acts chiefly through the medium of the 'apodème,' *e*, attached to the base of that joint.

*Flexor dactyli*.—In like manner the penniform muscle, in the swollen basis of the propes, draws, through the medium of the entapophysis, *g*, the dactylus, *s*, powerfully, in contact with the claw-like process of the propes, 5.

In the propes, or fifth joint, of the maxilliped, fasciuli of the muscular fibres are grouped to be inserted into the short basal apophyses of the lamelliform appendages (Pl. II A. fig. 4, *s, t*), which they tend to approximate, or to close upon or around the terminal chela (*ib. 7*). These plates, which radiate from the end of the 'propes' like the petals of a flower, are expanded by being pressed against the mud or sand, and seem to require muscles only for closing them, so as to facilitate the withdrawal of the limb. The application of the maxillipeds in locomotion was observed by W. A. Lloyd, Esq., the constructor of the Aquarium at Hamburg, of which he was for some years the conservator, and subsequently the constructor of that at the Crystal Palace, of which Aquarium he is now the manager.

At Hamburg, specimens of *Limuli* were kept alive from the year 1865 to 1870. From his observation of these Mr. Lloyd informs me, "The ulterior pair of limbs" (maxillipeds, VII) "are not employed for walking, but exclusively for burrowing. These limbs are terminated by four long stiff lobes of an oval or leaf-shape, jointed at the base, on the leg, and capable of being opened and closed in a four-radiate manner. When it wishes to burrow, these two limbs are, sometimes alternately and sometimes simultaneously, thrust backwards below the carapace, quite beyond the hinder edge of the shell; and in the act of thrusting, the lobes or plates on each leg encounter the sand, the resistance or pressure of which causes them to open and fill with the sand, a load of which at every thrusting operation is pushed away from under the crab, and deposited outside the carapace. The four plates then close, and are withdrawn closed, previously to being opened and charged with another load of sand; and at the deposit of every load the whole animal sinks deeper into its bed, till it is hidden all except the eyes. The great hiding-shield of a carapace again prevents one from seeing whether this excavating work is aided by the fanning motion of the abdominal false feet, as is the case with the British Lobster;

but I *think* there is such fanning, as I have seen signs of sand being driven through the sand-orifices as if urged by a current of water.

“The tail-spine of *Limulus* is used in locomotion in the following manner:—The animal having climbed up a rock in the Aquarium till it has got near to the top of a tank (which in Hamburgh contained thirty inches of water in depth perpendicularly), and having assumed a vertical position, leaves go its hold on the rock, and allows itself to fall backwards; but its downfall is instantly checked, and the creature propelled upwards by a downward flap of all the strong overlapping false feet; and when the impetus given by them has ceased, the animal sinks down, but is prevented from falling prone on the floor of the tank by alighting on the tip of the perpendicularly hanging-down spine. The moment that is done, and before the creature has lost its balance on the spine, the false feet make another flap, and give another impulse upwards and forwards; and so it progresses by a combination of swimming and hopping, or by a succession of slow hops on one leg, as it were; and all this time the position of the carapace is slanting, the top of the carapace inclining downwards at an angle of about  $45^{\circ}$ , the second segment of the body being at another inclination, and the tail-spine hanging freely vertically, as before mentioned; and by being brought down by its joint at various deviations from the upright one, the spine changes the direction of the march, while the false (swimming) feet effect the actual propulsion.

“The *Limulus* was fond of thus going about at night (generally remaining on the sand all day). Another use was made of the tail-spine, as a lever by means of which it righted itself when it fell off a rock on its back. The spine is then bent; *i. e.* its point is planted in the sand so that it makes an acute angle with the carapace, which is then so far raised that some of the feet are enabled to grasp a projecting surface, either longitudinal or vertical, or at some combination of the two; and the crab then turns over.”

The maxillipeds, no doubt, aid in burrowing, as observed by Mr. Lloyd; but the chief fossorial agent, as indicated by the size and disposition of the principal muscular masses, is the cephaletal digging-shield.

The operation of this is described in the subjoined note on the locomotion of *Limulus polyphemus* as observed by the Rev. S. Lockwood, Ph.D., in its native haunts (Rariton Bay, New Jersey, U. S.).

“The King-crab delights in moderately deep water, say from two to six fathoms. It is emphatically a burrowing animal, living literally in the mud, into which it scoops or gouges its way with great facility. In the burrowing operation the forward edge of the anterior shield is pressed downward and shoved forward, the two shields being inflected, and the sharp point of the tail presenting the fulcrum as it pierces the mud, while underneath the feet are incessantly active, scratching up and pushing out the earth on both sides. There is a singular economy of force in this excavating action; for the alternate doubling up or inflecting and straightening out of the two carapaces, with the pushing-purchase exerted by the tail, accomplish both digging and subterranean progression. Hence the King-crab is worthy to be called the ‘Marine Mole’” \*.

\* ‘The American Naturalist,’ 8vo, vol. iv. 1870, p. 257.



§ 4. *Nervous System*.—The chief part of the neural axis is in the form of an elliptic ring girding the œsophagus. Of this ring three views are given—one from above (Pl. V. fig. 1, *a*, *B*), one from below (Pl. IV. fig. 1, *a*, *β*), and one from the side (Pl. II A. fig. 1, *a*, *β*), in order to show, besides the shape of the part itself, the precise position of the nerves arising therefrom or connected therewith. For the origin of a nerve is an important element in determining the homology of the part it supplies; and such determinations have weight, as will be seen, in wider questions, extending, in the case of *Limulus*, e. g., even to class-affinity.

The part of the neural axis anterior to the œsophagus (Pls. II., III., V. *α*), and which, were the tube straightened and the mouth brought to its ordinary position at the fore part of the body, would be superior or dorsal in position, is an oblong mass, concave where applied to the tube (Pl. V.), convex on the opposite side (Pl. III.), 3 lines in length, and 4 lines in posterior or basal breadth, where its angles are continued into the side parts of the ring (Pl. II A. fig. 1, *β*). There is no trace of lateral bipartition of the superœsophageal or cerebral part of the neural axis. The substance of the ring shows the same axial or longitudinal extent behind as before the œsophagus; viewed from below, as in Plate III. fig. 1, it seems to extend rather further before contracting to form the ganglionic chord. The narrowest parts of the ring are at the sides of the œsophagus; but this is transversely; vertically the substance there is equal to that of the hind part of the ring (Pl. II A. fig. 1, *β*). Two commissural bands unite the lateral parts of the ring (Pl. V.). The ganglions (Pls. II A., IV., *δ*, *ε*, *ζ*, *η*, *θ*) are confined to the thoracetral region.

*Ocellar Nerve, n a*.—The first pair of nerves is the ‘ocellar’ (Pls. II., II A., III., IV., V., *n a*). They rise, with an interval of their own diameter, from the fore and upper part of the brain (Pl. V. *a*), diverge with a gentle curve as they advance, bend round the front convexity of the stomach (Pl. II A. fig. 1, *n a*), and ascend, converging to terminate each in its ocellus (ib. *a 1*). The length of the nerve is two inches.

*Ocular Nerve, n A*.—The second pair of nerves is the ‘ocular’ (ib. *n A*). Each nerve rises from a small conical process of the brain (Pl. V.), where the special quality of an optic ganglion may be surmised to dwell. An interval of the basal breadth of the swelling divides the ocular from the ocellar nerve. The ocular nerve curves upward, crosses the gizzard near the pylorus (Pl. II.), then more abruptly bends outward (Pl. V.), coasting round the apodeme (II) of the second limb, and retrograding obliquely to the compound eye, near which the nerve divides into a larger dorsal and smaller ventral chord. The dorsal division (Pl. IV. fig. 2, *d*) soon expands, and resolves itself into a fasciculus of nervules, which subdivide, and finally supply or form the retinæ of the lenses at the upper and hinder part of the compound eye. The ventral, which is also the anterior division (ib. *v*), is continued further before expanding and resolving into the plexus which supplies the retinæ to the lenses at the lower and fore part of the compound eye.

*Gastric Nerves*.—Two pairs of nerves arise posterior to the ocular pair. The nerves of the first pair (*n 3*, Pl. V.) pass forward, give filaments to the œsophagus and stomach, and are continued on into the hepatic and ovarian substance at the fore part of the carapace.

*First Epimeral Nerve.*—The nerves of the second pair (on the outer side of the symbol *n* 4, Pl. V.) diverge, extend along the fore part of the anterior low and simple apodeme (II), subdivide, and are lost in the tissues of that part of the segment answering, in position, to the epimerals\* of the type segment. The term ‘epimeral’ will, accordingly, be given to this and the succeeding serially homologous nerves.

*Second Epimeral Nerve.*—A somewhat larger nerve rises immediately behind the foregoing; the pair (Pl. V. *n* 5) slightly diverge and ascend, when each second epimeral nerve bifurcates. One branch coasts along the anterior apodeme, the other inclines toward the interspace between that and the second more prominent apodeme, supplies muscular fibres thence arising, and gives off a recurrent filament (*n* 6), traceable along the outer ends of the succeeding apodemes (II–VI, Pl. V.), at a little distance from them, as far as the seventh epimeral nerve, where this begins to ramify.

*Antennular Nerve.*—This nerve (*n* II, Pls. II., II A., III., IV.) rises from the under part of the base of the brain (*a* fig. 1, Pl. IV.), is rather larger than the second epimeral nerve, and supplies the first small forcipated pair of limbs—the homologue of the first or inner pair of antennæ in higher and more differentiated Crustaceans.

Two filamentary nerves rise from the interval between the antennular and antennal nerves at the beginning of the lateral parts of the ring (shown in Pl. IV.).

*Antennal Nerve.*—This nerve (*n* III) is more than twice the size of the antennular one; it supplies the second limb (Pl. IV. III), which is sexually modified in the male *Limulus polyphemus*. This limb, forcipated like the rest in the female, is the homologue of the outer and larger pair of antennæ in higher Crustaceans; and its origin is præ- or super-æsoophageal in *Limulus*.

*Third Epimeral Nerve.*—From the dorsal aspect of the lateral part of the neural ring rises the third ‘epimeral nerve’ (*n* 7, Pl. V.). It runs forward and outward above the interspace between the second (ib. II) and third (III) apodemes, and is resolved into a plexus of filaments beyond that interspace, which are lost in the glandular and other tissues of that region.

*Mandibular Nerve.*—The third limb-nerve (Pl. IV. *n* IV), of the same size as the second, comes off behind it, from the lateral part of the ring,  $\beta$ , and supplies the limb homologous with the ‘mandible’ (so called) in higher Crustaceans; which limb is marked IV in Plates II. & III., where the nerve is traced through the coxal and basial joints.

*Fourth Epimeral Nerve.*—From the dorsal aspect of the corresponding part of the neural ring is sent off the ‘fourth epimeral nerve’ (*n* 8, Pl. V.) having the same course and apodemal relations as the second and third of this series.

*Premaxillary Nerve.*—This, with a more posterior origin than the mandibular nerve, repeats the characters of that nerve, in relation to the fourth limb, or homologue of the ‘præmaxilla,’ or first or anterior maxilla, in higher Crustaceans. The nerve (*n* V) is shown in Plates II. & III., entering and traversing the ‘coxa’ and ‘basis’ of the limb marked V. This limb is sexually modified in the male of *Limulus moluccanus*, but not in the species here dissected.

*Fifth Epimeral Nerve* (*n* 9, Pl. V.).—This repeats the relative position of origin to

\* Owen, ‘Lectures on Invertebrata,’ p. 298.



the premaxillary nerve which the antecedent one (*n* 8) bears to the mandibular nerve, and holds the same relation in its course to the apodemes IV & V. It forms the plexus beneath that of the optic nerve, beyond which the filaments are lost in the tissues there. The optic nerve crosses dorsad of the first four epimeral nerves in its course to the compound eye.

*Postmaxillary Nerve*.—The fifth limb-nerve (*n* VI, Pls. II A. & IV.), with a more posterior origin and a course more obliquely backward, repeats in limb VI—the homologue of the postmaxilla, or second maxilla, in higher Crustaceans—the characters of the ‘premaxillary nerve’ in relation to limb V.

*Sixth Epimeral Nerve* (*n* 10, Pl. V.).—This repeats the same relative position of origin to its answering limb-nerve as does *n* 9; it is continued further obliquely backward before bending outward to its interapodemal space, and bifurcates before entering there, the hinder division descending to supply the strong adductor muscle of the sixth limb (VII in Pls. II A. & IV.).

*Maxillipedal Nerve* (*n* VII, Pls. II A. & IV.).—The nerve supplying that limb has its origin between the postmaxillary nerve and the beginning of the abdominal ganglionic chord  $\gamma$ . It repeats the character of the antecedent limb-nerves in relation to its own articulated appendage, which is the homologue of the ‘maxilliped’ in higher Crustaceans.

*Palpal Nerves*.—At the interspace between the origins of the postmaxillary and maxillipedal nerves, as in that between the latter and the ganglionic continuation of the neural centre, arise filaments which supply the spinigerous process or ‘palp’ of the compressed denticulate haunch-joint (Pl. II A. figs. 2 & 5, *p*).

*Chilarian Nerve* (Pls. II A. *n* X, & IV. *n*\*). This rises between the origins of *n* VII & *n* VIII; it is appropriated to and richly ramified in the leaf-like spinigerous appendage, articulated behind the base of the maxilliped, and closing posteriorly the circumoral armature. The serial homology of the chilarian with the palpal nervules lends some countenance to that of the appendage, so supplied, being a detached spinigerous process or ‘palpus’ of VII.

*Seventh Epimeral Nerve* (*n* 11, Pl. V.).—This arises dorsad of the origin of the maxillipedal nerve, passes backward and outward to its proper apodeme (VI), where it divides, and, running onward, ramifies to supply the tissues in the hinder produced angles of the cephaletron.

*Eighth Epimeral Nerve* (*n* 12, Pl. V.).—This is one of the same system of dorsal nerves, succeeding the seventh; it passes backward and slightly outward along the dorsal margin of the seventh apodeme (VII), and dips into the articular depression between the cephaletron and thoracetron.

*Opercular Nerve*.—The hindmost pair of cephaletral ventral nerves (*n*, Pl. II A. & *n* VIII, Pl. IV.) is given off at or just before† the continuation of the neural ring into the ‘ganglionic chord.’ The nerves of this pair run along the sides of the latter for about 8 lines, then slightly diverge, curve outward, and send off one or two filaments laterally, before descending to penetrate the base of the anterior or opercular leaf-foot,

† This lends countenance to the idea that the ‘opercular limb,’ VIII, is the last of the cephaletral series.

or coalesced pair of limb-appendages of the segment anchylosed to the back of the cephalotron.

The corresponding dorsal pair of nerves (*n* 13, Pl. V.) also course along the sides of the ganglionic chord before diverging to ramify in the middle third of the interspace between the cephalotron and thoracetron.

The ganglionic chord ( $\gamma$ , Pls. II A., IV.) extends backward about an inch before its first ganglion ( $\delta$ ) is formed; this is followed by three others ( $\epsilon$ ,  $\zeta$ ,  $\eta$ ) and a terminal swelling ( $\theta$ ) situated about an inch and a half from the joint of the tail-spine. The interganglionic tracts average in length about  $2\frac{1}{2}$  lines, slightly shortening as the chord recedes.

Each of the four anterior ganglions gives off two pairs of principal nerves, one dorsal and anterior (*n* 14–17, Pl. V.), the other ventral or posterior (*n* IX–XII, Pls. II A. & IV.), these terms not being absolute, but meaning the approximate relative position of the places of union of the nerves with the ganglion. The dorsal nerve is a serial repetition of the antecedent epimeral ones. It passes outward along the contiguous apodemal interspace, on emerging from which it divides; the posterior branch quickly subdivides; the anterior branch continues further before subdividing; all these filaments incline obliquely backward before distributing themselves among the tissues of their corresponding abdominal segments. The dorsal nerves (*n* 17, Pl. V.) from the fourth ganglion run backward a short way before inclining outward. A filament of each of the thoracetrans epimeral nerves can be traced to the movable side-spine of its segment.

The ventral nerve goes obliquely outward and backward to the space or joint between its own segment and the one in advance, penetrates the branchial leaf-limb at the part or moiety of its own side, distributes many filaments to the basal joint, and is continued on through the second and third joints, before being finally resolved in the fourth and terminal joint (Pl. II A. *n* IX–XII). More minute filaments are sent off, usually between the origins of the two chief nerves, from the four ganglions.

The terminal ganglion ( $\theta$ , Pls. II A. & IV.) represents the coalescence of the nerve-centres of at least three segments. Its anterior dorsal pair of nerves (*n* 18, Pl. V.) traverse the interval between the fifth (XII) and sixth (XIII) thoracetrans apodemes, in a course more obliquely backward than the antecedent pairs. The corresponding anterior ventral nerves (*n* XIII, Pls. II A. & IV.) supply the sixth pair of leaf-limbs or fifth branchial pair (XIII). Below the origin of this pair, nervous filaments (*r*, Pl. II A.) pass off to the lower fourth of the intestine.

The second ventral pair (*n* XIV, *ib.*) is chiefly distributed to the fibres of the flexor muscles of the tail-spine, arising from and occupying the soft, rather tumid tract, which resembles a leaf-foot soldered down to form the covering of the hindmost part of the ventral surface of the thoracetron.

The third pair of principal nerves from the terminal ganglion represents a bifid continuation of the neural axis (Pl. IV., *l*). After a course of about three lines, each sends off a nerve (*n* XV, Pl. IV.) belonging to the ventral series, which supplies the hindmost or postanal region of the abdomen affording the articular surface for the tail-spine.



After sending off the above nerve, each continuation of the chord forms an oblong loop (*ib.*  $\kappa$ ), which, prior to the removal of the vascular sheath, looks like a ganglionic swelling\*; beyond which the chord ( $\lambda$ , Pls. II A., IV.) continues along the side of the tail-joint, and, on entering the cavity of the tail-spine (c), resolves itself into a fasciculus of fine nerves (*ib.*  $p\ell$ ), resembling the 'cauda equina' of anthropotomy. But in this bundle a principal filament, or continuation of the chord (Pl. II A.  $\mu$ ), can be traced about a third of the way down the spine. These nerves seem to constitute the major part of the tissues in the hollow of the spine, and render a marvellous supply of neurine to so hard, inflexible, and seemingly insensible a part.

Each chord,  $\lambda$ , from the ganglionic loop sends off nine nerves, four directed toward the ventral (Pl. IV. fig. 1,  $p\ell$ ), four towards the dorsal (Pl. II A. fig. 1,  $a$  1-4) region of the spine: the ninth nerve being of larger size, claims to be the continuation of the bifid neural axis. If the dorsal and ventral divisions be regarded as those of four nerves serially homologous with such divisions of antecedent primary pairs, they would indicate as many segments coalesced in the fore part of the spine. The ninth nerve and its divisions supply in a similar way the rest of the tail-spine.

Are the phenomena of this terminal part of the nervous system of *Limulus* devoid of homological significance? It seems to be otherwise, for any thing that one can see needing such supply of nerves in the interior of the hollow spine. All, however, that embryology has yet shown of the development of this part is, that in the interval between exclusion and the first moult it buds out of the posterior part of the thoracetron, does not shrink up to it, and only feeble or doubtful traces of a segmentation have been noticed in the embryonal but late-growing 'pleon.' Nerve precedes crust in blastemal differentiation: the earlier tissue obeys the type, the later tissue the adaptive departure therefrom. A superficial glance catches the result as a 'spinous process;' deeper insight discerns the body-joints masked by the outer connation. Neither development, rightly understood, nor adult structure gives any countenance to the notion that the tail-spine of *Limulus* is a mere process or appendage growing from the dorsal part only of the terminal segment of the thoracetron.

Seeing the relations of the pleonal nerves as continuators of the neural axis, and the like relation of the artery of the spine to the dorsal vessel, I long ago concluded the spine itself to be a continuation of the series of body-segments, to be serially homologous therewith, and not with their 'appendages.' The coccygeal style of the frog's endoskeleton† is analogous to the tail-spine of the King-crab's exoskeleton. The antecedent part of the thoracetron ( $B''$ ) wherewith the spine is articulated has no limbs. Is it also part of the pleon? and does the postganglionic part of the neural axis indicate the extent of such part?

In anatomizing, in 1843, my first-received specimens of *Limulus*, the details of the nervous system were followed out by my then anatomical assistant, Mr. Henry Goadby, and well exemplify his peculiar skill and patience.

The nearest approaches to the type of nervous system above described we found to be,

\* As represented by Van der Hoeven, *op. cit.* pl. iii. fig. 2 c.

† Owen, 'Anatomy of Vertebrates,' vol. i. p. 49, fig. 44 c.

not in the Crustacea most resembling *Limulus* in general shape and proportions (the Brachyures, *e. g.*), but in Arachnids and Myriopods.

In a Scorpion (*Buthus africanus*) the two cerebral or superœsophageal lobes are fused together, send off nerves to the chelicera, or antennal homologues of the limbs II in *Limulus*, and to the eyes; they are connected behind with the stomatogastric nerves, and laterally, by means of short and thick 'crura,' with the subœsophageal mass. This, as in *Limulus*, represents the ganglionic centres of several pairs of nerves, including those of the chelate palps, the homologues of which come off in *Limulus*, as in other Crustacea, from the superœsophageal mass. The four pairs of cephalotral limbs succeeding the 'palpi' in *Scorpio*, also derive their nerve-supply from the subœsophageal part of the annular centre. From this are continued the ventral chords along the thoracetreron, successively developing seven closely fused pairs of ganglia; the terminal chords distribute, in the pleon, or jointed tail, pairs of nerves to the right and left, and are traceable to the bent and perforated tail-spine, representing a 'telson,' but forming, by a mysterious modification, the poisonous weapon of the Scorpion.

The nervous system of this 'air-breathing Merostome' has been well figured by Newport\*; and I supply additional illustrations of that of a Myriopod†, which may represent a condition of the nervous system in the Trilobites.

The superœsophageal or cephalic portion of the neural axis in *Julus terrestris* (Plate II. figs. 6, 7, 8) is more transversely extended than in *Limulus*, and is less obscurely divided into the right and left ganglions or side-lobes, of which the upper and outer ends are produced as short and thick optic lobes, which are resolved halfway toward the compound eyes into a plexus of filaments, distributed, as in *Limulus*, to the component ocelli. From the fore and outer part of each cephalic lobe two distinct nerves proceed to the short 7-jointed antenna of its side; below these a pair of nerves proceed to the palpless mandibles (fig. 6). From the hind and underparts of the cephalic lobes the thick continuations of the neural axis descend and girt the gullet, beneath which they become resolved into two chords or rings: the anterior one anastomoses with its fellow, forming a simple ring; the posterior and larger chords converge at an acute angle, to be continued into the ventral body-chord, which shows little of a ganglionic structure. The converging head-chords are, however, united by a transverse commissure before retrograding to the ventral body-chord. This commissure and the anterior ring recall the filamentary cerebral commissures in *Limulus* (Plate V.); the anterior œsophageal or pharyngeal ring in *Julus* is also homologous with that shown by Lyonnet in the larva of *Cossus ligniperda*.

The stomato-gastric system begins by a single slender median chord from the hind notch at the cerebral lobes, and immediately forms, or is in connexion with, a third slender ring girding the œsophagus (*ib.* figs. 7 & 8), from the middle and upper part of which the trunk-nerve of this system passes a short way back on the dorsal aspect of the stomach before it divides. The divisions diverge at an angle of 45°, then bend, and are continued

\* Philosophical Transactions, 1843, plate xii.

† *Julus terrestris*, outlined in my 'Anatomy of Invertebrates,' p. 356, fig. 144, 8vo, 1855.



backward parallel with each other (fig. 8), running upon the dorso-lateral parts of the wide and straight alimentary canal.

§ 5. *Digestive System*.—This system of organs includes a ‘mouth,’ with instruments for seizing and comminuting the food, a ‘gullet,’ a ‘stomach,’ an ‘intestine,’ with vent and accessory glands, of which, in the present genus, the ‘liver’ only has been recognized.

The mouth is median, and situated, as in other masticatory Crustacea, on the under surface of the body; it is, as in them, surrounded by modified portions of articulate limbs, working laterally; but these, in number and concentration, are paralleled only by the extinct Merostomes (Cut, fig. 14, *e. g.*): the mouth, it may be remembered, also resembles that in Spiders in respect of its distance behind the fore border of the cephalotron (Pl. II. fig. 2). The circumoral integument, in *Limulus*, is yielding and elastic, cushioned out with soft tissues, including fibres interlacing and susceptible, if muscular, of giving change of form and position to the thick and prominent lips, endowing them with movements, small in extent, but various, for seizing the morsels of food torn by the haunch-palps or ‘carders’ (Pl. II A. *p. p.*). The thick labial epithelium yields to such movements by transverse folds or indents. The mouth opens on a plane not only behind that of the basal attachment of the antennules (or ‘first pair of chelate appendages,’ II), but also clearly behind that of the basal attachments of the ‘second pair,’ or antennæ (III). Nor can those of the ‘third’ pair be said to be placed ‘posterior to the mouth.’ Their nerves arise rather in advance than behind the œsophageal tube; and their haunches are on the transverse parallel of the anterior lip, as shown in Pl. II A. fig. 1, *n* IV, & fig. 2, *p* IV. In a general way the mouth of *Limulus* may be said to occupy the interspaces of the haunches (*coxae*) of the right and left limbs, III–VII, these limbs being crowded or close-packed at their basal articulations, on each side of the mouth, whence they diverge to their pincer-shaped tips. The haunches are compressed, as if squeezed together; and their under or median borders are produced, with a convex margin, which, with more or less of the contiguous flattened surface, is beset with sharp, short, slightly curved spines. These are not mere processes of the chitine, but are slightly movable, their base being articulated to a pit. The spiny plate, or ‘palp,’ of the first of these jaw-feet (III) is inclined backward, and overlaps part of that of the second (IV), which has a like relation to the third (V); this is set more transversely, and is wedged, as it were, between the second and fourth. The haunch of this foot (VI) has a similar position between that of the third (V) and the somewhat less spiny haunch of the last pair of legs or ‘maxillipeds’ (VII). This complex series or circle of carding-instruments is bounded in front by the three-jointed antennæ (II), having the same chelate structure as in the multiarticulate ones of *Pterygotus* (Cut, fig. 14); it is closed behind by the ‘chilaria,’ or pair of appendages marked \* in Pls. II A. & IV.

The operation of these circumoral instruments in the living King-crab is thus described by a close and accurate observer:—“The food is held immediately under the mouth by the nippers of the anterior pair of feet (II), aided, if necessary, by those of some of the others. The manducatory limbs then begin an alternating motion of their haunches upon the food, by drawing one of those rasp-like joints against the opposite one of the

same pair, the food being held between the two. This chewing by means of these opposing rasps reminded me," writes Dr. Lockwood, "of the hand carding-process, in which the card held by the right hand is brought towards and against the one held in the left hand, the wool being between, when the right hand card is held still, and the left hand duplicates the motion, and so on. The fine particles rasped off by the incurved teeth pass into the mouth" \*.

The tumid and wrinkled margins of the mouth quickly contract to an œsophagus about a line in diameter. This tube (Pl. II A. fig. 2, *æ*) curves upward and forward in a course of  $1\frac{1}{4}$  inch; then dilates into a conical proventricular cavity (*r*) extending downward, about 5 lines in depth by  $3\frac{1}{2}$  in breadth at the base. From the fore part of the base a second short canal ascends, to terminate by a slight vascular prominence in the stomach (*s*). The epithelium, or modified chitine, continued from the mouth along the gullet and proventriculus, becomes suddenly thickened in the stomach, and is disposed in numerous transverse ridges. The muscular coat of the stomach is concomitantly strengthened, attaining at one part a thickness of 3 lines. The pyloric end (*mt*) projects as a truncated cone, 4 or 5 lines long, into the dilated beginning of the intestine (*i*). The truncate apex of the pyloric cone is slightly tumid. The epithelium lining that part has resumed its thinness and subtransparency.

The intestinal tunics appear to be reflected from the base of the pyloric cone; they define a dilated beginning of the canal, and gain a slight thickness of the muscular coat as they contract to the common size of the intestinal tube, the area of which is about 5 lines in transverse, and 3 lines in vertical diameter. The tube goes nearly straight to the vent (Pl. II A. fig. 1, *i*, *v*); but, about halfway there, it contracts transversely (Pl. I. fig. 1, *i*), and exchanges its oval for a circular section, with a diameter of  $2\frac{1}{2}$  lines. Near the vent it again expands, chiefly transversely; and the muscular coat there gains somewhat in thickness. The vent (Pl. II A. fig. 1, *v*) is a transverse slit with tumid margins, just anterior to the joint between the thoracetrone and pleon.

The contents of the alimentary canal were pulpy and scanty. The principal food of the *Limulus polyphemus* is stated by Dr. Lockwood (*loc. cit.*) to be Nereids, routed by the cephalotribral limbs out of the mud or sand displaced in the act of burrowing.

The only gland in communication with this canal is the liver. It is of great size; its minute terminal acini are compactly massed together, and occupy most of the space in the cephalotrone not given to other organs, mainly the generative, the ramifications of which interlace with the hepatic lobes. A part of this mass is shown at *n*, fig. 1, Pl. I.; but it extends forward to the space anterior to the stomach, and backward by a narrow tract (ib. *n'*) on each side of the intestine in the thoracetrone. The lobes, or larger groups of acini, form a close-packed series on each side, corresponding in the main in number with the apodemal spaces and the epimeral nerves. The least unsuccessful trials of injecting the terminal canals and acini indicated the greater transverse and less longitudinal extent of the hepatic lobes or primary divisions of the gland (as shown at *n''*, fig. 1, Pl. I.). The gathering tubes of the initial or acinal ducts of these lobes course, in the main, transversely toward the intestine until they quit the lobe, when they

\* Lockwood (Rev. S., Ph.D.) in 'The American Naturalist,' vol. iv. p. 260 (1870).



converge abruptly to form the terminal duct. The anterior of these receives the tributary ducts of the four chief anterior divisions of the liver; the posterior terminal duct is formed by the union of the same number. The ducts of two or three of the anterior lobes unite to form that which enters the main or terminal anterior duct; those from the four posterior lobes unite and enter the posterior terminal duct by two canals. The arrangement, however, shown in the subject of fig. 1, Pl. I., may be varied in other specimens: but the principle of segmental constitution, as here exemplified by the secondary ducts, will be found, I doubt not, in all *Limuli*. It indicates the liver to have been developed, in relation to the primitive composition of the cephalotron (Cut, fig. 5), of antero-posteriorly succeeding portions, there being a pair of livers or hepatic lobes to each of five or more embryonal segments. The confluence of the ducts interestingly exemplifies the way of subsequent concentrative growth characteristic of the mature and procreative individual.

The bile is conducted to the intestine by two terminal ducts on each side: the first pair (fig. 1, Pl. I., & fig. 2, Pl. II A., *l*) open upon the sides of the beginning of the tube, where it contracts to the ordinary calibre; the second pair (*ib. m*) open about 9 lines beyond, and nearer the dorsal part of the intestine.

As in the King-crabs, certain Spiders (*Epeïra*, e. g.) have their ventral mouth † provided anteriorly with a chitinous plate, ‘labrum’ or ‘prostome,’ and posteriorly with a labium or ‘metastome,’ which is soldered to the cephalotral plastron, not bifid and movable as in *Limulus* (Pls. II., II A., III., & IV. \*). The œsophagus rises, at first, vertically dorsad, then bends back at a right angle, traversing in that part of its course the neural ring before expanding into the stomach. This cavity is, in most spiders, produced into cœcal appendages, which, in some, extend into the basal joints of the cephalotral limbs. The bile-ducts open into that part of the intestine which traverses the thoracetron (‘abdomen’ of arachnologists). The proportion of difference to resemblance must be kept in mind when speculating on the degree of affinity of Xiphosura and Arachnida.

§ 6. *Sanguiferous System*.—The dissection of *Limulus* was commenced from that aspect or plane of the body next to which, in Invertebrates, is the part of the neural axis called ‘superœsophageal,’ and which, as it supplies nerves to the organs of sense, answers to the brain in Fishes. As in these Vertebrates, also the removal of the neural or dorsal part of the skeleton (Pl. I. fig. 2) exposes the vascular system (*ib. a, a*) analogous to the so-called ‘aorta’ of Fishes, and homologous with the ‘dorsal vessel’ in Insects. In *Limulus* the walls of this vasiform heart exhibit muscular and valvular structures, for the same purpose or office as those of the vertebrate ‘heart.’

In a specimen dissected, with a carapace, or upper crust of the two chief parts of the body, 9 inches in length, the heart was 4 inches 8 lines in length (Pl. I. fig. 2, *a, a*). It was included in a delicate membranous sac analogous to a pericardium, but forming, in fact, the wall of a venous sinus. This wall consists of two layers. One may be properly termed a ‘tunic:’ it includes extremely delicate fibres, chiefly transverse, but reticularly interwoven in a fine cellular bed, the inner surface of which has been the seat of formifaction, or vital crystallization, of particles from the contained fluid, forming an

† *a*, fig. 109, ‘Lectures on Invertebrata,’ 8vo, 1843.

epithelium\*. The whole resembles a fine arachnoid membrane (a portion of this pericardium is shown at *b*, fig. 2, Pl. I.).

The heart is fusiform, widest at its hinder third, gradually narrowing, transversely, to its fore end, which is  $2\frac{1}{2}$  inches from the fore part of the cephalotron, more rapidly contracting to its hind end, which is  $1\frac{1}{2}$  inch from the joint of the tail-spine. In the vertical diameter (Pl. II A. fig. 1, *r*, *r*) the hinder contraction is more gradual.

The heart-wall consists of an outer, thin, smooth, compact coat, and a wall of striate muscular fibres consisting of a thin outer longitudinal layer and a thicker transverse or circular series. The wider part of the heart shows traces of an epithelial lining, due to the action initiated or invited by a surface in contact with the formifying material in solution. The arachnoid coat of the pericardial sinus is reflected over the outermost proper tunic of the heart, and is continued into the venous ostia (Pl. I. fig. 2, *c'*, *c*), where it gains thickness.

These ostia are sixteen in number, arranged in seven pairs at the sides, but towards the dorsal surface, of the heart, with a terminal eighth pair. The hinder 'ostia' are rather nearer together than the others. The muscular tunic in the intervals of the ostia (Pl. II A. fig. 1, *r*, *r*) is about a line in thickness, but thins off rapidly at the two ends of the heart. Each 'ostium' (ib. *o*, *o*) is provided with a pair of narrow semilunar valves, placed with the intermediate slit almost transversely to the axis of the cardiac tube.

The foremost artery (Pl. I. fig. 2, *h*) runs to the 'ocelli' (*a* 1), is there connected with, or seems to enclose, the nerve; it then bends down, following the curve of the carapace to the angle formed by the upper with the flat under surface of the digging-shield, near which angle the artery is reflected backward and cannot be further traced as a distinct tube. On each side the origin of the 'ocellar' artery arises one of double the size (ib. *e*, *e*), which, diverging from its fellow, curves outward and downward over the fore part of the intestinal canal (Pl. II A. fig. 1, *s*): it gives off, in this course, a branch which ramifies upon the gizzard, a second to the intestine and liver, the main trunk being continued to the nervous annular centre (ib.  $\beta$ ), where it expands, and combines with its fellow of the opposite side to form a sheath for that centre analogous to a 'dura mater.' This rather loose sheath is continued along the ganglionic ventral chord, and is prolonged, like a loose neurilemma, upon the nerves sent off therefrom, as it is upon those in connexion with the annular centre.

Fine size-injection being thrown into the 'heart' from behind forward, appeared to give a rich display of arterial ramifications. But dissection showed that the contents of the seeming arteries ceased to be the simple injected matter where the 'gastric arches' (ib. *s*) reached the nervous ring (ib.  $\beta$ ); for here the coats of the artery become thinned, the injection lining them as a thin flake of colouring-matter, and, at the same time, covering a thinner membrane which formed the 'neurilemma,' or chief layer of the delicate tunics of the nervous matter of the neural ring†. The same condition was presented by the seeming abdominal arterial trunk continued backward from the neuro-arterial circle (Pl. V. *a*, *B*, to or. of nerve *n* 19). On slitting open the coats of the blood-

\* Owen, 'Anat. of Vertebrates,' vol. iii. p. 499.

† Preparation, No. 1303 c, Physiol. Series, Mus. Coll. of Surgeons.



vessel, and washing out the flake of injection, the ganglionic nervous chord was exposed in its interior\*. The same result followed the like perquisition of the smaller ramifications of the vascular system into which the injection had penetrated, and engendered the conviction that the main pair of arteries had but a brief course as such†, becoming resolved, on reaching the neural ring, into blood-sinuses—a condition which prevails throughout a great proportion of the vascular system of *Limulus*. The whole nervous system, save where the terminal twigs are lost in the tissues, is bathed in the blood of these sinuses, which retain the appearance of ramified vessels, through their relations to the nerves as the vascular envelopes of these‡. Elsewhere the sinuses expand, lose the character of tubes, or vessels, occupy the interspaces of viscera and muscles, initiate from a subcardiac sinus the ramified branchial system of vessels, and return the blood from all parts to the pericardial-like sinus enclosing the heart.

A pair of arteries is sent off near the anterior pair of ostia, and are closely connected with the much larger veins emptying the neighbouring sinus into the corresponding parts of the pericardial one. These arteries (Pl. I. fig. 2, *f*′) pass outward and forward, and subdivide into branches, which are lost upon the epimeral nerves. The next pair of arteries correspond with the second ostial vein (ib. *f*′): I was unable to trace them far. This vein courses outward near the hind border of the cephalotron, bends forward at *n*, and runs parallel with the lateral or ocular ridge as far as the compound eye: its branches are short, and speedily expand into sinuses§. A pair of arteries are obscurely indicated,

\* The neurine thus seems to be small in proportion to the thick neurilemma, as Gegenbaur remarks; but he did not recognize the share taken by the arterial tissues in this sheath:—“Bezüglich des feineren Baues soll die schon oben angeführte dicke Umhüllung des Schlundringes erwähnt werden, derzufolge der eigentliche Nerventhail des Schlundringes relativ klein erscheint.” *Op. cit.* p. 241.

† They are shown as cut off from the arches and lost upon the brain in Pl. V.

‡ This interesting stage in the differentiation of nerves and vessels was demonstrated in my Hunterian Lectures of 1852, ‘Organization of the Entomostraca illustrated in the *Limulus*,’ Lecture xvi. *Crustacea*, ‘Synopsis,’ March, 1852, and is briefly enunciated in the volume on INVERTEBRATA as follows:—“The sides of the great œsophageal ring are united by transverse commissural bands: but the most remarkable feature of the nervous axis of this Crustacean is its envelopment by an arterial trunk. A pair of aortæ from the fore part of the heart arch over each side of the stomach, and seem to terminate by intimately blending with the sides of the œsophageal nervous ring. They, in fact, expand upon and seem to form its neurilemma; a fine injection thrown into them coats the whole central mass of the nervous system with its red colour.”—*Lectures on the Comparative Anatomy and Physiology of the Invertebrate Animals*, by Prof. Owen, F.R.S. (second edition, London, 1855, Lecture xvi. p. 310). A similar condition, requiring injection for distinguishing the vessel from the nerve, is pointed out in the Scorpion (*op. cit.* p. 449). Gegenbaur, in his histological treatise on *Limulus* (*op. cit.* p. 241), remarks:—“Auch die peripherischen Nerven sind sämmtlich von einer dicken Hülle umgeben, die sogar noch makroskopisch erkennbar ist.”

§ That an arterial canal accompanies the vein is indicated by the course of the blood, as observed by Packard in a living larva of *Limulus*:—“I could not see the walls of any of the arteries; and indeed the arterial blood seemed to flow in channels exactly like the venous sinuses, as in the arteries which pass around the margin of the carapace the blood-disks were seen to pass by irregular currents towards the front edge of the margin. The anterior aorta could not be detected in the young *Limulus*; but on each side of the end of the heart the blood could be seen rushing out and in, and with a general course downwards, beneath the œsophagus, while a current of blood flowed on each side of the stomach and œsophagus, and thence went out at a considerable angle to the edge of the carapace, where it divided, sending a branch around under the ocelli, and another along the outer edge of the cephalic shield, and again subdivided opposite the second pair of cardiac valves” (Pl. I. fig. 2, *c*, *f*′), “one current following the edge of the cephalothorax” (ib. *n*), “and the other going on towards the heart” (ib. *b*′). “The abdominal arteries,

arising near the last pair of 'ostia,' passing obliquely outward and backward. The posterior or 'pleonic' artery (Pl. II. fig. 1, *t*) has more definite tunics and holds a longer course than those from the fore part and sides of the heart. It is wavy at its beginning, in relation to the varying directions of the tail-spine in its flexile movements upon the body. The artery having entered the body of the spine, continues its course, as such, along the dorsal side of the cavity, through two thirds of its length, then subdivides and blends with the sinuses continued from the ventral chord and investing the 'cauda equina' of the tail-spine.

The veins, or venous sinuses with the least indefinite form, are those that course along beneath the medi-lateral ridges of the cephalotron in association with the arteries (Pl. I. fig. 2, *n, n*), and those which follow and lie near the margins of both cephal- and thorac-etra. The latter return their blood by the posterior veins (ib. *r*), united by the median channel (*s*) with the pair in advance, *q*; their common trunk opening into the hind part of the pericardial sinus, *b'*.

§ 7. *Respiratory System*.—The gills consist of thin membranous plates of a broad semi-oval shape; there are from 150 to 200 in each gill or group, the number diminishing in the hinder ones. The gills are in pairs, attached to the upper, hinder, or inner surface of the proximal joints or broad coalesced plates of the last five thoracetransal limbs (IX–XIII, Pls. II., II. A, III. and IV.).

The branchial plates overlap each other from before backward. The anterior and exterior one is the smallest; the others progressively increase to a little beyond the middle of the series; the hindmost again diminish, but in a less degree; the whole mass has the full oblong or irregular oval form shown in fig. 2, Pl. V. Each plate is strengthened by a chitinous filament along its free border, thickest where this is exposed, so that the length of the gill is greater at its free or floating side than along its attached base: the free margin is also ciliate.

Each gill-plate consists of two layers or membranes, united along the chitinous border, and also by numerous filaments so far apart as to divide the interspace into reticular canals or cells, smallest at a subcentral space (fig. 3, *a*), and affecting a concentric arrangement as they approach the free borders of the gill-plate. The two constituent layers of the branchial plate may be regarded as productions or duplicatures of the delicate skin of the upper or inner surface of the lamelliform limb.

From a venous sinus along the base of attachment of the gill-plates \* the blood passes

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represented by powerful currents of blood issuing from between the last two pairs of cardiac valves, are directed obliquely outwards and backwards. The caudal aorta sends a current nearly to the tip of the spine, the venous sinuses returning it along the sides. The simple arrows mark the course of the returning currents, which flow from all parts of the body towards the valves."—*Development of Limulus polyphemus*, pl. v. fig. 27, p. 171.

This admirable memoir appeared subsequently to the reading of my paper 'On *Limulus*' before the Linnean Society; and the Report given in the Number of 'Nature' for January 25, 1872, is quoted by Dr. Packard at p. 201. Dr. Packard notes that the heart "beats ninety times a minute," in the larva after the first moult.

\* "Il paraît exister une libre communication entre ces diverses poches respiratoires; car, en introduisant de l'air dans une de ces duplicatures, on voit non seulement s'écarter les lames de la même branchie, mais même se gonfler toutes les branchies, ainsi que l'espace membraneux entre les pattes abdominales."—V. der Hoeven, *op. cit.* p. 19. The intercommunicating passage is the basal sinus, related to the gills, physiologically, as a 'branchial artery.'



freely into the interlamellar spaces; whence it enters the vessels coursing along the border of each plate, from the inner side towards the outer side (fig. 2, *a*) where the vessel is largest. Here appears to begin the returning system of branchial veins on the fore part of the base of attachment. These veins ascend and converge on each side of the intestine, and traverse the pericardial sinus to enter directly the heart by the five pairs of ostia at the widest posterior part of that organ.

The muscles which divaricate the branchigerous limbs, and at the same time separate the gill-plates and expand their cavities to the extent permitted by the interposed columns, act as inspiratory ones, inviting the flow of blood from the abdominal sinuses into the cavities of the gill-plates. This action may be supposed to take place when the King-crab is moving or resting in its atmosphere of sea-water. The muscles which approximate the branchigerous plates and press them against each other and the thoracetron, will close the ciliate slits leading to the gills, will compress those organs, and tend to squeeze the blood from the reticulate interspace of their constituent lamellæ. Such movement must be 'expiratory,' and also effective in defending the delicate surfaces of the branchial membranes from the atmosphere of muddy or sandy sea-water when the King-crab is burrowing either for food or concealment.

§ 8. *Reproduction of Parts*.—Of the power of reproduction of limbs or other appendages, after mutilation, I have not found recorded evidence; but such may be inferred to be possessed by *Limulus* from the reproduction of the entire crust, as in other and higher members of the class. According to Dr. Lockwood \*, the King-crab moults several times during the first year, perhaps five or six times between its exclusion in June to the setting-in of cold weather. Like other Crustacea, it moults more frequently during the earlier and more rapid period of growth than afterwards. The young *Limuli* acquire an inch in length in the first year: it is then that, after the moult, the second pair of limbs are observed to have gained the sexual form in the male. "In older *Limuli*, just before the time of exuviating, a separation occurs between the marginal rim and the perimeter of the anterior shield." "To the unaided eye the rent is imperceptible, but opens on exertions of the animal; and at this opening it emerges from the old shell"†. A specimen which had accomplished this moult measured  $9\frac{1}{2}$  inches in the short diameter of the cephaletron, while the vacated shell was but 8 inches by the same measurement. This exuviation was observed in the month of August: but Dr. Lockwood gives an instance of a *soft Limulus* having been dredged up in the month of February, whence he thinks they may moult twice a year.

§ 9. *Generative System*.—In *Limulus* the sexes are distinct; the male is smaller than the female; and in both, the generative organs lack those accessory parts that relate to intromission in some higher Crustaceans.

The ovarium is a system of ramified tubes and cavities, occupying chiefly the dorsal region of the body; it extends along the median part of the thoracetron, and expands laterally in the cephaletron.

Parts of the ovary are single and median; the rest consists of parial symmetrical lateral ramified tubes, chiefly situated in the cephaletron.

\* 'The American Naturalist,' vol. iv. No. 5. July 1870, p. 242.

† Ibid.

The hindmost cavity (Pl. IV. fig. 6,  $q$ ) is a longitudinal tube, commencing by a blind end above the rectum; it extends forward, expands, and bifurcates about the middle of the thoracetron; the branches at first diverge, then bend inward and reunite, sending back into the interspace of the bifurcation a short blind sac. From the base of this heart-shaped portion the bifurcate tubes are continued forward, slightly diverging, leaving a mid space for the heart and intestine as they cross the articulation between the thoracetron and the cephaletron. About two inches in advance of the second bifurcation each tube expands laterally into a triangular cavity, from the outer and fore angles of which the ramified systems of the lateral loops,  $q''$ , are continued. A small branch is sent off from the outer side of the dilatation. Three or four tubes converge from its fore part, and anastomose† to form the anterior single symmetrical cavity,  $q^*$ . This is oblong, subquadrate, subdepressed, and subreticulate. It is longitudinally channelled above, by the fore part of the heart resting thereupon, this part of the ovary being interposed between the heart and intestine (Pl. IV. figs. 1 and 2,  $q$ ). It seems to have been developed in or from the last remnant of the included germ-mass. From the hinder and outer angles of the antero-median part of the ovary proceeds the tube, which passes outward and backward, joins that from the fore part of the lateral expansion, and curves outward and forward to meet and inosculate with a similar retrograde branch from the fore and outer angle of the antero-median lobe. From the outer side of these ovarian loops (Pl. I. fig. 2,  $q^{**}$ , and Pl. IV. fig. 6,  $q''$ ) proceed four or five branches which inter-ramify with the hepatic lobes. The branch tubes ( $q^*$ ) continue from the fore part of the antero-median sac; and its loops are continued, subdividing and reticularly anastomosing, along the sides of the gizzard to the fore part of the cephaletron.

Each of the main parial oviducal canals, before converging to the anterior reunion, dilates and sends outward and backward a wide tube, which after sending off, or rather receiving, three large tubes ( $q^{**}$ ) is continued backward as the common oviduct (Pl. I. fig. 2,  $o$ ; Pl. IV. fig. 6,  $o$ ). The hindmost of the three large tubes passes outward and backward to near the outer ends of the joint between the cephaletron and thoracetron, and there curves forward beneath the lateral cephaletral ridge, and receives the ova from the parts of the ovary extending to the lateral margins of the cephaletral cavity. The foremost of the three branches collects the ova from the deeper-seated interapodemal parts of the ovarium, the intermediate branch those from the dorsal level above and exterior to the apodemata.

The numerical correspondence of the lateral tributaries to the main median or sub-median receptacles of the ova with the neural indications of the segmental constitution of the two chief divisions of the body, is less obvious than in those of the hepatic masses. This may be due to the later period of development of the genital factories.

The part of the ramified ovarian system to which the term oviduct is here applied is the tube,  $o$ , continued from the common stem of the three last-described tubes, and

† 'Lectures on Invertebrata,' ed. 1855, p. 329: shown, in *Maia*, in fig. 135,  $a'$ ,  $b'$ . Anastomoses between the right and left system of ovarian-tubes were also noticed by Gegenbaur (*loc. cit.* p. 247), who well remarks on this evidence of crustaceous affinity:—"Durch diese Verbindung beider Ovarialhälften reiht sich *Limulus* an viele andere Krustenthier an, wo gleichfalls ein unpaarer Abschnitt der inneren Genitalorgane vorhanden ist."



passing backward, inward, and downward, across the cephalo-thoracetral joint, to the part of the upper or inner surface of the 'opercular' limb, VIII, shown in fig. 6, Pl. IV. The termination here of the oviduct ( $p$ ) was rather prominent: the outlet is transverse, and formed by tumid labia, with the inner surface transversely plicate.

The bifurcation of the hind part of the ovary before passing from the thoracetron to the cephalotron, relates mechanically to the accommodation of the cardiac and intestinal tubes during the frequent and forcible inflections of the two great body-chambers upon each other. The laden ovarium, instead of being pressed down upon the heart (as it would have been if it had been continued as a single median and vertically parallel viscus across the joint where the cephalotron was depressed at an angle with the thoracetron), slips, by its division, on each side the heart during the inflection. A similar relation to convenience of package governs the forward extension of the ovarian bipartition in relation to the main parts of the heart and intestine.

The most significant difference between the female organs of *Limulus* and those of the higher or malacostraceous squat-eyed Crustaceans is the absence of the dilated part of the oviduct forming the copulatory pouch, or 'spermatheca,' which absence relates to there being no intromission in the act of impregnation in *Limulus*.

In the male, the testes are ramified and subreticulate, like the ovaria, and occupy almost an equal extent of the two great cavities of the body. The sperm-ducts open upon corresponding position of the opercular plate (Pl. IV. fig. 8,  $p$ ), their termination being on a smaller but rather more prominent cone of thin yellow chitine, at the apex of which the sperm-tube terminates by a whitish bilabiate orifice (Pl. IV. fig. 7,  $b$ )\*.

§ 10. *Development*.—It may not be unacceptable here to give the results of the observations of the Rev. Sam. Lockwood, Ph.D., on the generation of the American King-crab (*Limulus polyphemus*), condensed from the account he has consigned in the under-cited periodical†.

In Rariton Bay, New Jersey, U. S., the King-crabs spawn in the month of May, June, and July, at the periods of highest tides. In that operation they ascend from the depths in pairs, the male holding on to the carapace of the female by his hook-feet (Pls. II. & III. III). Arrived near the line of breakage of the highest tidal waves, "the female digs a hole in the sand, and drops her spawn into it, upon which the male emits the fecundating fluid, and the nest is then deserted, the parents returning seawards with the retreating tide"‡. Occasionally a pair are left exposed by the tide, which they then

\* Dr. Packard describes the spermatozoa as having a broad oval body, sometimes contracted before the anterior end, and posteriorly suddenly terminating in a filament about four times as long as the body ('On the Development of the *Limulus polyphemus*,' 4to, Memoirs of the Boston Soc. of Nat. History, vol. ii. p. 156).

† 'The American Naturalist,' vol. iv. No. 5, for July, 1870.

‡ Ib. p. 264. Notes on the living *Limulus* are appended to the paper "On the Relationship of the Xiphosura," &c., by Henry Woodward, Esq., F.G.S., communicated to the Geological Society December 20th, 1871; and in reference to a remark by the author, that Crustacea, "as a rule, appear to fecundate the ova by a true union before the eggs are discharged from the ovaries," the Editor of the 'Quarterly Journal' (February 1872) refers to a paper by M. Chautran, showing "that the eggs of the common Crayfish are fecundated after expulsion from the oviducts" (p. 48). I gather, however, from that paper, that although ova may be impregnated after passing from the oviducts, there is a more definite copulatory act than in *Limulus*, in which spermatozoa might find their way into the oviducts.

hasten to overtake if unmolested. By the action of the water the eggs, about half a pint in quantity, are covered up with sand.

This thoughtful observer calls attention to the advantage of the choice of 'spring-tides,' in the lengthened exposure of the sand-covered spawn to the vivifying warmth of the sunshine during the 'neap-tides.'

On the 26th May, 1869, he obtained new-laid impregnated eggs, the hatching of which was accomplished slowly, owing to "the absence of those conditions of agitation, variation of water-depth, and sometimes complete exposure to air and sunlight, consequent on the tidal flow" \*. July 18th the opaque exochorion dehiscence or cracked, disclosing the white, pellucid, spherical endochorion. The included embryo consisted of two parts (cephaletron and thoracetron); but, as first observed by the masterly crustaceologist Milne-Edwards †, the 'pleon,' or tail-spine, was undeveloped.

Before hatching, the cephalettron is divided by an anterior mid dent into two lobes, and the ocelli are not distinguishable; its segmental constitution, or nature, is indicated by six transverse linear indentations across the middle third; the compound eyes appear as pigment-specks outside the second and third indentations. The smaller thoracetron is triangular, with linear indications of the segments along the middle third of the dorsal surface. The resemblance of the embryo *Limulus*, at this stage, to *Sao* is noted by Dr. Lockwood; but the cephalettral limbs are conspicuous, "it has the feet quite advanced." "In the course of two or three days their extremities reach beyond the edge of the carapace." "The embryo had its two segments inflected; and with short intervals of rest (not many minutes at a time), kept up a very active revolving motion within its pellucid prison" ‡. August 3rd, seventy days from spawning, an embryo left the ovum. It measured  $2\frac{1}{2}$  lines in length and 2 lines in width. Except for a little space in front, "the notch there being now obliterated and filled up by the part supporting the ocelli" (ib. a), the margin of the cephalettron is armed with spines, about twenty-five on each side. The thoracetron is now nearly as broad as the base of the cephalettron, to which it is articulated: its free border is semicircular, and provided with tufts of setæ. The growth of the tail-spike had not commenced. The liberated embryo "at once began to shift for itself, making a persistent effort to burrow like the parent."

Such a spectacle was almost equivalent to a long retrospect in time—a watching of the living *Prestwichia*, e. g. (Cut, fig. 17), on the old ocean-shore of Coal-brook Dale. "The segmentary lines afford a very distinct trilobed character to both shields." The spiny and setaceous fringe finds its counterpart in *Hemiaspis* (Cut, fig. 18). "In the presence of the ocelli and the high-up position of the large sessile eyes, we have *Eurypterus* shadowed forth" § (Cut, fig. 13). "The want of an articulated tail was soon apparent in the case of our little *Limulus*. The slightest obstacle turns it on its back,

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M. Chantran states that, in this act, "the female lies on her back, bending forward the tail, and making a hollow, into which the ova are passed, the male depositing the spermatophora upon the plates of the tail-fan and on the plastron of the female, whose abdominal appendages secrete a greyish viscous fluid."—'Compte Rendu de l'Acad. des Sciences,' 15 Janvier 1872.

\* 'The American Naturalist,' vol. iv. p. 265.

† 'Journal de la Société Philomathique,' Novembre 1838.

‡ Lockwood, *loc. cit.* p. 266.

§ Id. ib. p. 267.



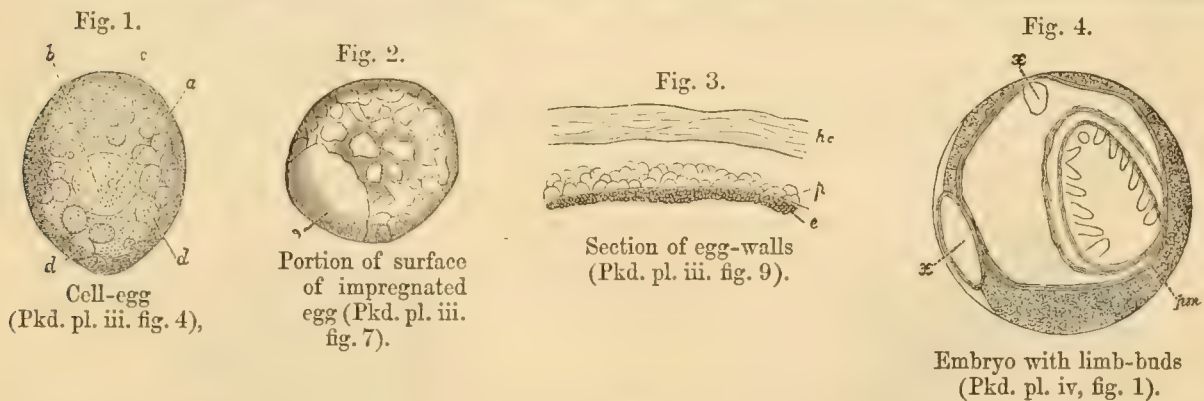
when, not having this organ (which the adult uses so effectively in such emergency), the little thing begins a vigorous flapping of the branchial plates. This causes it to rise in the water; then, by ceasing the agitation, it at once descends with a chance of alighting right side up"\*. Eighty-two days after spawning, a young *Limulus* moulted. "A few minutes sufficed for it to withdraw itself from its baby-suit; in this act it rested a little while, with the caudal appendage, now formed, only half withdrawn from the old shell"†.

The extricated animal is  $\frac{1}{4}$  of an inch in width, and its tail is  $\frac{1}{20}$  of an inch in length. The tail is formed bent under the thoracetron, is at first curved, and "requires some hours to straighten out"‡. The setaceous fringe of the thoracetron is replaced by teat-like or half-developed spines. The spiny fringe of the cephaletron is gone. The tail is at first somewhat stumpy, almost ovoidal in transverse section, "more distinctly marked with lines of segmentation than is that of the adult"§. As the young *Limulus* "travelled on the mud before this moult, it made tiny rows of toe-tracks, leaving a plain unmarked space between the rows. Now it moves with tail depressed, and makes a median line, dividing the toe-tracks into two series"||.

The year following the collecting of the ova, Dr. Lockwood records the interesting fact that certain ova at the bottom of one of the jars, "which had never been in contact with the sunlight," still retained the embryo alive and revolving; these having been transferred to "new sea-water and clean sand, with a good exposure," were hatched; and the larval *Limulus* left the egg within two weeks of a year after oviposition and impregnation of such egg¶.

Dr. A. S. Packard\*\*, from observations on impregnated ova of *Limulus*, transmitted to him by Dr. Lockwood, adds details of intraovular steps of development, and gives acceptable figures of these and of the excluded larva.

Formifaction aggregates the protoplasmal beginning of the ovum into a central mass



of larger and denser granules, constituting the nucleus (cut, fig. 1, *b*), within which is

\* Lockwood, *loc. cit.* p. 268.

† Id. *ib.*

‡ Id. *ib.*

§ Id. *loc. cit.* p. 269.

|| In quoting this observation, I am duly impressed by the "caution for the interpreters of the 'Protichnites,' seeing that the same species, at different ages, may make widely different tracks."—*Id.* p. 273.

¶ Id. *ib.* p. 272. This result recalls the arrest of development of Tadpoles kept in the dark.

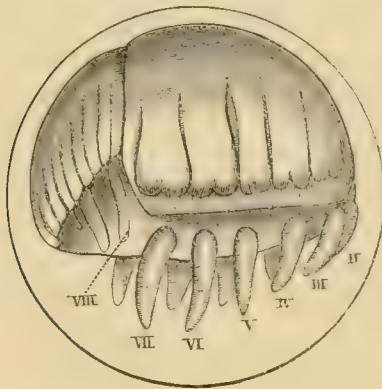
\*\* "The development of *Limulus polyphemus*," in *Memoirs of the Boston Society of Natural History*, vol. ii. 1872. (This excellent memoir was read November 16th, 1870.)

the hyaline nucleolus, *a*. Round this is the mass of germ-yolk, *c*, in which are recognizable granules round other centres definable as yolk-cells, *d*. Impregnation of such ovum is followed by denser blastodermal aggregates (cut, fig. 2, *c*). Peripheral differentiation and condensation next define upon the blastoderm (*e*, cut, fig. 3) a protoderm (ib. *p*) within the chorion (ib. *hc*).

The formation of the blastoderm accords with that of freshwater *Gammari* and of Arachnids, the yolk not undergoing segmentation. It is not uniformly diffused, but the seat of development is localized in an aggregate of more numerous and smaller blastodermal cells (ib. *e*).

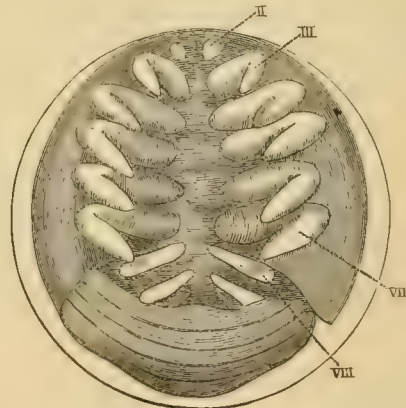
The embryo is first recognizable, as such, by parial groups of these cells (cut, fig. 4) on the surface of the protoderm (ib. *pm*; "amnion," Brandt). These groups, by their gradational difference of size, indicate, what later development shows, that they are the beginnings of the cephaletal limbs. Between and a little in advance of the smaller pair a round speck appears, which denotes the mouth. Portions of yolk (ib. *x, x*) are detached before the formation of the blastodermic skin. This advance takes from one to two weeks after exclusion under ordinary favourable influences, and is accompanied by secession of the protoderm.

Fig. 5.



Embryo, with cephaletron and thoracetreron defined. (Pkd. pl. iv. fig. 19.)

Fig. 6.



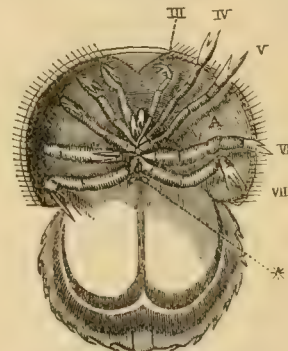
Embryo at the same stage, from below. (Pkd. pl. iv. fig. 19 A.)

Fig. 7.



Embryo just before hatching. (Pkd. pl. v. fig. 24.)

Fig. 8.



Newly hatched young. (Pkd. pl. v. fig. 25 A.)

A similar heaping up of cells, as a ridge, marks out the hind margin of the cephal-



etron. The indications of segmental structure on its dorsal surface, or carapace, are marginal and transversely linear, due chiefly to the hepatic lobes seen through the transparent skin; they denote six segments (cut, fig. 5). The buds of the anterior pairs of thoracetransal limbs (ib. VIII) next appear; and the joints of the longer cephalotransal ones (II-VII) become more marked. The embryo now rotates in its moulted protoderm. The definition of the thoracetron is speedily followed by the out-budding of a third pair of limbs. The compound eyes (cut, fig. 7, 1) appear as white dots; the ocelli (ib. *a*) are next discernible on the first segment. Behind the six cephalotransal segments there are now eight thoracetransal ones, and a ninth, pleonic, as broad as long. These are defined upon the periphery of the spherical embryonal mass.

At this stage the chorion cracks; and sea-water, endosmotically filtering through the protoderm, expands it, and allows free flotation to the rotating embryo. The heart appears as a pale streak, extending from the front edge of the cephalotransal to near the opposite end of the thoracetron, along the median dorsal depression. The reaction of the sea-water upon the intra-ovular embryo, combined with excentric pressure through growth, is manifested by the peeling off of a thin skin. The body becomes flattened as it broadens; the median region of the tergum rises, and interrupts the segmental lines; the compound eyes project from the boundary ridges between the median and lateral regions, and the three-lobed character of the carapace is manifested. The 'sternal' surface recedes from view, in profile, and the hollow (cut, fig. 8, *A*) lodging the mouth and maxillipeds begins to be established. At this stage the spatulate appendages of the penultimate joint of the limb VII. appear as simple spines, and the terminal forceps is complete in this, as in the antecedent limbs. Now, also, the 'chilaria' appear as rather flat oval tubercles closing behind the sternal or 'oral' groove (fig. 8, \*).

In this state of development the young *Limulus* escapes from the 'protoderm' (amnion, endochorion). The cephalotransal is about half as long as wide, its margins are fringed with cilia, from pits on their upperside. About three weeks after hatching, the skin is shed; the thoracetron shows its marginal notches and movable spines, the latter shorter than in the adult. A fourth pair of lamellate limbs appears. The pleon now projects from the mid notch of the eighth segment, its base embracing the vent, which opens upon it; its apex is subacute, and its length about thrice its basal breadth. A second moult was observed between the middle and latter end of August.

The sum of these observations shows the progressive acquisition of the mature characters of the King-crab without undue development attended with subsequent loss or curtailment of parts in relation to a phase with habits of life markedly different from those of the adult—in other words, without 'metamorphosis.' In this respect *Limulus* follows the course shown in *Astacus fluvialilis* † and some other Crustacea, as well as in Arachnids and Cephalopods.

Dr. Anton Dohrn ‡ has also recorded notes on the ovum, embryo, and young of

† Comp. fig. 4 with fig. 136, p. 336, 'Lectures on Invertebrata,' and fig. 5 with fig. 137, p. 337, ib.

‡ "Untersuchungen über Bau und Entwicklung der Arthropoden," 'Jenaische Zeitschrift,' Band vi. Heft 4 (1871), p. 582. Of other contributions by this excellent observer to the embryology of the Crustacea I may cite:— 'Die embryonale Entwicklung des *Asellus aquaticus*,' 8vo, 1867; 'Untersuchung. üb. Anat. u. Entwickl. d. Arthro-

*Limulus*, afforded by specimens preserved in alcohol, transmitted to him by Dr. Packard. They are confirmatory of the accuracy of the observations of the able American embryologist as detailed and illustrated in the work above cited. Dr. Dohrn premises a German translation of Dr. Lockwood's memoir in the 'American Naturalist,' and of the 'Abstract' (which appeared in the same periodical) of Dr. Packard's Memoir. The chief characteristic of the contribution by the German carcinologist lies in the point of view which he has taken of the phenomena. It is a development of that sketched out as follows, in my 'Lectures on Crustacea' of 1843 and 1858. "To what end, it may be asked, tends all this discussion concerning the affinities of animals that have long ceased to exist? How are we concerned with it in considerations relative to the generation and development of the actual Crustacea? To this I have to answer, that it is only by a knowledge of the transitional larval forms of these that we come rightly to comprehend the nature and affinities of the extinct Trilobites, and that *our knowledge of the most interesting relations of actual larvæ requires a previous knowledge of the forms of their class that have heretofore existed on this planet*"\*. This view is developed and illustrated, with large assumptions, as follows, by Dr. Dohrn:—"Fritz Müller himself made the first decided application of this 'law,' viz. that the embryological development was nothing more or less than a short, though not always exact, recapitulation of the history of all the ancestors of the organism in question—by tracing the different orders of the Crustacea back to their common ancestor, the famous *Nauplius*, that little crustacean larva that quits the egg and is afterwards gradually developed into the well-known diversified and more highly organized forms"†.

It may not be out of place here to recall what is understood in plain matter of fact by the term *Nauplius*, as contrasted with its transcendental signification.

The young of Entomostraca, with ciliate natatory limbs (cuts, figs. 9 & 10) more or less like those of the parent, want, when hatched, the protective bivalve-like cephalotracheal shield and some other parts of the adult, yet soon show characters which enable the student of the group to refer them to their species, the full diagnosis of which they yield, as in *Limulus*, after successive ecdyses.

The first systematic observer of the small representatives of the subclass ‡, not knowing the genetic relations of his subjects, referred the young of some species to distinct genera—those of *Cyclops* (*Canthocamptus*) *minutus* e. g. to a genus *Amydone*, and the hexapod stage of *Cyclops quadricornis* to a genus *Nauplius*. Later observations have led to these larvæ being relegated to their proper genera and species §. *Nauplius saltatorius*, O. F. M. (fig. 10), is the young of *Cyclops quadricornis*; *Nauplius bipes* (fig. 9) is the larva of *Apus*

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poden, I. Cumaceen,' 8vo; 'II. Pycnogoniden;' 'III. Daphniæ,' 8vo, 1869; 'Die Schalendrüse u. embryon. Entwickl. d. Daphnien,' 8vo, 1869; 'Ueberreste d. Zoëastadiums in d. ontogenet. Entwickl. d. verschied. Crustac.-Fam.' 8vo, 1870; 'Unters. üb. Bau u. Entwickl. d. Arthropoden,' I. & II., 8vo, 1870.

\* 'Lectures on Invertebrata,' 8vo, ed. 1855, p. 333.

† Dr. A. Dohrn, in the 'Academy' for Nov. 1, 1871, p. 429.

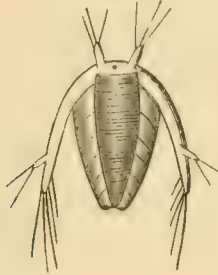
‡ 'Entomostraca, seu insecta testacea, quæ in aquis Daniæ et Norwegiæ reperit, descripsit et iconibus illustravit, Otho Fred. Müller,' 1785.

§ See the excellent work 'The Natural History of the British Entomostraca,' 8vo, 1850, by W. Baird, M.D., F.L.S.



*canceriformis*: other *Nauplii* and *Amymonæ* are entered among the synonyms of the full-grown parents to which they severally belong—as, *e.g.*, to *Canthocamptus minutus*, Baird, *C. stromii*, *C. furcatus*, *C. chelifer*, &c. The ‘*Nauplius*’ of *Balanus*, *i. e.* the young of that Barnacle after quitting the egg, is a free ‘hexapod,’ with relatively larger swimming-limbs, furnished with more numerous and relatively longer setæ than in *N. saltatorius*\*.

Fig. 9.



*Nauplius* (young of *Apus*) *canceriformis*.  
(After Baird, *op. cit.* tab. i. fig. 2.)

Fig. 10.



*Nauplius saltatorius* (young of *Cyclops*).  
(After Baird, *op. cit.* tab. xxiv. fig. 9.)

Thus it appears that *Nauplius* is not a ‘thing’ but a ‘name.’ That is, the term means not one but many things, and all of them known more truly or scientifically under other ‘nomina’ of multitude, both generic and specific.

It is essential in this part of my memoir to hold an intelligible idea of what is signified by *Nauplius*, in reference to its application to the question whether the embryonal development of *Limulus* is a “recapitulation of the history of all its ancestors,” or merely a manifestation of the phases of its own specific growth—and if the latter, whether any of those phases resemble not a *Nauplius* only, but other species or genera of Crustacea, more, and in more essential characters, than they resemble later phases or the generic characters of the parent.

At the phase of development of *Limulus* (fig. 4) which is called the ‘*Nauplius* stage’ †, the resemblance is as follows: the limbs are restricted to the part of an undivided body answering to the later-defined cephalotral division, as yet not distinctly marked out. The correspondence of the embryo *Limulus* to the young Entomostracan is carried no further. The cephalotral limbs in the former are mere buds; the terminal joint is bent on the proximal one; there is no trace of setæ, not the slightest indication of any transitional natatory structure or function of such embryonal limbs. The mouth opens, almost, in its limuline relations to the antennules (II) and antennæ (III); and these already show their characteristic difference of size. Their next step is to gain the prehensile chelate structure, as in the adult. What the “famous *Nauplius*” may be I have not been able to make out; but if the stage in question really represents any “common ancestor,” it certainly is not the *Nauplius* of carcinologists. It may also be remembered that *Limulus* differs from the parents of *Nauplii*, *i. e.* Copepods, Phyllo-pods, and other Nauplian Entomostraca, in the eggs being left to hatch in a sand nest, not carried about in egg-bags.

\* C. Spence Bate, “On the Development of the Cirripedia,” in ‘Annals and Magazine of Natural History,’ 2nd Series, vol. viii. (1851) p. 324, pl. vi. fig. 1, *Balanus balanoides*; fig. 5, *Balanus perforatus*.

† Packard, *loc. cit.* pp. 163, 202.

Shortly after the foregoing so-called "Nauplius-stadium," the thoracetral limbs begin to show; and this is termed the "Zoëal stage." The phenomena supporting or suggesting that phrase are, that in the Limuline larva both cephalotron and thoracotron are defined, with limbs, and that the pair of compound eyes are discernible on the former. But the *Zoëa* of the Brachyura\* is framed, like the *Nauplius* of the Entomostraca, for free natatory life. Its limbs are exclusively 'cephalotral,' and are terminally branched and ciliate. The thoracetral segments show no limbs; and the terminal or 'pleonal' one is bifurcate and ciliate, for assisting the parial limbs in swimming (cut, fig. 11).

At the subsequent, so-called, "Trilobite stage" (fig. 7) †, the young *Limulus* has a superficial resemblance to some of the Trilobites, and especially when these are at perhaps a corresponding period of development. The body of the so-called larva *e. g.* of *Trinucleus ornatus* (cut, fig. 12, *a*) consists of two shield-like and somewhat semicircular-shaped parts joined together by their truncate or transverse borders. The upper surface of the foremost, answering to the 'cephalotron' of *Limulus*, has also a raised median region defined from the two lateral regions—a configuration which suggested the term 'Trilobite.'

But here the resemblance ceases in the main.

The hind division in the Trilobite (fig. 12, *c*) is not the homologue of that of the larval *Limulus*. The 'thoracotron' of Trilobites (ib. *B*) is developed, like the supernumerary

Fig. 11.

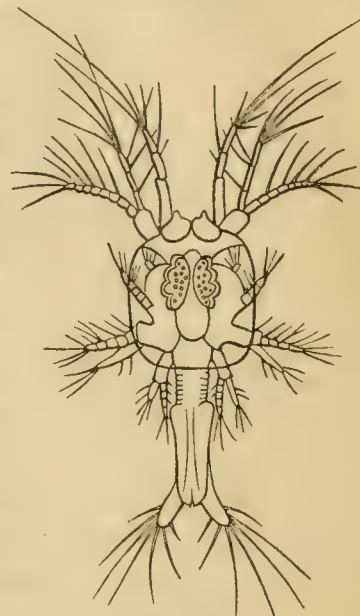
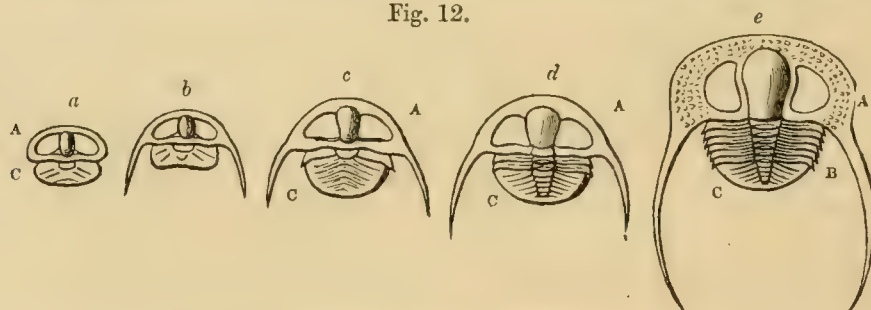
Larva or "Zoëa" of *Penæus*.

Fig. 12.

Larvæ of *Trinucleus ornatus*.

segments added to the primary 'eight' in *Julus*, by successive formation in the germinal space between the cephalotral (ib. *A*) and pleonic or pygidial (ib. *c*) divisions of the body. The cephalotron of the Trilobite has no articulate appendages. It is doubtful, to say the least, whether any were attached to the thoracotron (ib. *B*). What have been supposed to be such in that part of *Asaphus platycephalus* ‡, are not lamelliform, operculate, or

\* Anat. of Invertebrata, 1855, p. 340, figs. 138, 139.

† "Das Stadium welches wir jetzt betrachten wollen, können wir am Besten und Bezeichnendsten das 'Trilobitenstadium' benennen."—A. DOHRN, *op. cit.* p. 588.

‡ By E. Billings, Esq., F.G.S., Quarterly Journal of the Geological Society of London, vol. xxvi. pl. xxvi. fig. 1 (May 1870); also by H. Woodward, Esq., F.G.S., Geological Magazine, vol. viii. (1871) pl. viii.



branchigerous at any period of the Trilobite's existence; but, if the ridged (what a carpenter would call 'beaded') inferior borders of the eight thoracetrans segments have not been so misinterpreted\*, are slender, filamentary, cylindrical, jointed ambulatory limbs, terminated by a claw†. Under either alternative the difference is great as compared with the coalesced pairs of broad lamelliform articulate appendages of the thoracetrans of the larval (fig. 8) as of the mature *Limulus* (Pls. II. & III.), and still greater when the Trilobitic larva, with its pleon or pygidium for the second body-part, (fig. 12, *a, b*), is compared with what is termed the "Trilobitenstadium" of the *Limulus*; in which stage one sees, with the thoracetrans for the second body-segment, beneath it already developed three or more of the lamelliform limbs, on the second and third of which the gill-plates have begun to appear‡. This is far from being a 'Trilobite;' and nothing is gained to science by putting figurative expressions for facts. In the inductive school of biology, the notion that a higher form traversed a series of lower forms in the course of its development has ceased to be set forth, save under duly modified terms§. I am under the impression (and it is an agreeable one to the mind searching solely for intelligible and demonstrable conclusions) that few now dispute the fact that each individual of a given species is such *ab initio*, and takes its own course to the full manifestation of its specific characters, agreeably with the nature originally impressed upon the germ. A King-crab does not, any more than a perch, a dog, or a man, begin to be such only when the zoologist discerns the respective characters of the parent, but is such even before embryologists detect their earliest dawn. The embryo *Limulus* derived its nature and the potency of growth according to the specific pattern from the moment of the impregnation; and each step of development moves to the consummation of the pattern as its end and aim||. The generic character is indeed significantly soon shown in the budding *Limulus*.

The first steps, like those in all segmental (whether articulate or vertebrate) animals, recall the work of crystallization, and illustrate growth by repeated samenesses. These show the results of formifaction, aggregated in series of similar heaps of organic atoms (fig. 4) before the specific affinities begin formally to operate thereon and plainly to show themselves to the eye. No sooner, however, can one of these heaps, or pairs of heaps, be recognized as budding limbs, than in such series the first is seen to be Limuline by its halting growth (fig. 6, II); the second (III) pushes on outside these, the basal joints of the 'antennules' (II) being at the interspace of those of the 'antennæ' (fig. 8, III), according to the King-crab's pattern.

Further back in that interspace opens the mouth (fig. 6). It is at no developmental stage typical as a transient manifestation of the ordinary position of the mouth in an annulose animal; that is to say, it is at no time terminal—but as soon as it opens (fig. 4), testifies by its inferior position that it is the mouth of a *Limulus*, not of any other or any lower form.

\* I offer this alternative with diffidence, as I have not had the opportunity of examining the exceptional specimen.

† According to H. Woodward's restoration, in 'Geological Magazine,' July, 1871, pl. viii. fig. 1 *a*.

‡ Packard, *loc. cit.* p. 170, pl. v. fig. 26.

§ See the concluding Lecture of my course on "Invertebrata," of 1843, 8vo, p. 367.

|| Anat. of Vertebrates, vol. i. p. xxi.

Thus, in the existing representative of Xiphosura, the embryo or larva is neither a *Nauplius* nor a *Zoëa*, nor a Trilobite: it is a *Limulus*, exhibiting the characters of such in stages of development or growth corresponding to the period of incubation at which the immature creature may be examined.

§ 11. *Conclusion*.—That the Trilobite, like the *Limulus*, possessed articulate limbs, has, however, been advocated not only by interpretation of appearances in an exceptional instance, but by appeal to the laws of coexistence\*. I would submit, however, the following remarks bearing upon the correlation of vision with other ways and means of locomotion.



*Limulus* possesses the pair of relatively large compound eyes, set high upon the lateral parts of the cephalotracheal carapace; and besides these, it has the pair of small anterior simple eyes: it looks forward and upward, and commands, like the guns of a demilune bastion, a like range in the horizontal sweep. And yet the prevalent impression, from the position and proportions of its subcylindrical jointed limbs, is that they subserve the needs of digestion much more than those of locomotion. No observer has yet testified to their capacity of uplifting the body from the ground, whether dry or submerged, and of bearing it along by successive steps, as do the jointed legs of the Isopod, the Lobster, or the Crab. Some of the pairs are obviously incapable of such locomotive functions. The last pair (VII. in all the figures) may help to push the body along the sand,

as the oar serves to shove off a boat; but that is all.

*Eurypterus* (fig. 13) and *Pterygotus* (fig. 14) possess, like *Limulus*, both the antero-median ocelli and the medio-lateral compound eyes. In *Pterygotus* the antennæ are



forcipated members for prehension of food, as in *Limulus*. The three succeeding pairs of cephalotracheal limbs are still less capacitated, through their proportionally smaller size and concomitant slenderness, for gradatorial movement of the body. They are adapted to rout out of the sand or mud, disturbed by the spade-shaped head, the objects of food which the front pair is modified to seize. The larger terminal pair of limbs are more decidedly natatory in form than are the last cephalotracheal lamelligerous pair (Pl. IIA, figs. 2, 4, VII) in *Limulus*. In *Eurypterus* the cephalotracheal limbs anterior to the lamelliform natatory pair seem to be alike in structure, unless the antennal forceps has been wanting in the fossils, and must have had functions as limited as are their size and strength.

These considerations weigh with me in checking a tendency to conclude that the Trilobites, because they had large compound eyes, must have had articulate ambulatory limbs of as strong a texture,

\* "The large compound sessile eyes, and the hard, shelly, many-segmented body, with its compound caudal and head-shield, differ from any known Phyllopod, but offer many points of analogy with the modern Isopods; and one would be led to presuppose the Trilobites possessed of organs of locomotion of a stronger texture than mere branchial frills."—H. WOODWARD, *Geological Magazine*, vol. viii. p. 523.



whether crustaceous or chitinous, as their body-segments. That sixteen slender freely movable filamentary limbs, as restored by Mr. Woodward\*, each nearly  $1\frac{1}{2}$  inch in length, attached by a flexible joint no bigger than a pin's head, and divided into seven movable segments by six other joints, in a Crustacean that may have undergone, to say the least, some disturbance between death and fossilization—that the eight pairs of such articular appendages should remain and be found symmetrically and regularly arranged across the ventral surface of the fossil, with intervals, if not parallel to, yet corresponding in length with those of the thoracetrans segments—presents itself to my mind as much less probable than that the narrow parallel ridges which constitute the observable phenomena should have had such extent of attachment to the ventral surface of the several segments as to offer the requisite physical resistance to displacement and to loss of original regularity and symmetry of position, such as the specimen of *Asaphus platycephalus* described and figured by Billing† actually presents to view. If this Trilobite possessed the ambulatory legs ascribed to it, it could hardly be an exception, in this endowment, to its order, and traces of such limbs, in divers conditions of displacement, would be common.

The varied and usually more or less dislocated positions of the jointed limbs in the fossil Merostomatous crustaceans would lead one to expect a like condition in other families of palæozoic fossils possessing similar appendages‡.

The difficulty of getting a clear view of the nature and affinities of *Limulus* at the stage of anatomical investigation which had been reached before the date of the present paper, and the need of such further help as could be given by one occupying himself therewith by the way, as it were, and in the brief snatches of leisure which administrative duties and the cultivation of more congenial fields of original research might permit, will be appreciated from the fact that one who has devoted to this question so much pains, and skill, and dialectic ability as the indefatigable crustaceologist Dr. Anton Dohrn has left his conclusions as to the class-characters *e. g.* of *Limulus* in a condition, to say the least, not so supported as to command the common consent of his fellow labourers. For myself it is a plain duty, and under responsibility for opportunities of dissection so kindly and liberally afforded by American friends, to give my reasons for dissenting from the view of *Limulus* being so far *Arachnidan* as to require, with its extinct allies, to be placed as a distinct group, not of, but by the side of, the *Crustacea* §.

\* Geol. Mag. viii. 1871, pl. viii. fig. *t a.*

† *Loc. cit.*

‡ The above considerations incline me to view, as the more probable interpretation of the appearances in this fossil that given by the accomplished naturalist Dana, to whose writings, and especially those on the Crustaceous class, I am indebted for much interesting and valuable knowledge.

§ “*Limulus* ist zunächst verwandt mit den Gigantostirken; beide erscheinen verwandt mit den Trilobiten, obwohl diese Verwandtschaft nicht in alle Details nachgewiesen werden kann. Die morphologisch-genealogischen Beziehungen dieser drei Familien zu den Crustaceen lassen sich vor der Hand nicht feststellen, bleiben vielleicht für immer zweifelhaft.—Sonach bleibt uns nur übrig, diese drei Familien unter einem gemeinsamen Namen, wofür ich Häckel'schen Ausdruck ‘Gigantostiraka’ möchte in Vorschlag gebracht haben, selbständig zu constituieren und im System neben die Crustaceen zu stellen.” . . . “Was bei Savigny andeutungsweise, bei Strauss-Dürckheim mit Einseitigkeit ausgesprochen wurde, das tritt also jetzt unter dem Gesichtspunkte der Descendenztheorie von Neuem auf. Die Verbindung der *Arachniden* mit den *Crustaceen* soll durch *Limulus* und die ihm verwandten Eurypteriden gegeben

In these questions the nervous system yields important indications. If it were a fact that "in *Limulus* only the foremost pair of limbs was innervated from the superoesophageal ganglion, the rest deriving their nerves from the abdominal ganglionic chain"\* , the advocate for its elimination from the Crustaceous class would have an argument of weight for the affinity of *Limulus* and its extinct allies with the Scorpion and Spider.

The allies here referred to are those possessing cephalic limbs the general characters of which are repeated in *Limulus*.

The anatomical investigations of well-preserved mature King-crabs, the results of which are given in a previous section (§ 4) of the present memoir, have convinced me that *Limulus*, like other Crustacea, does derive the nerves of its two anterior pairs of cephalic limbs (II, III) from the cerebral (=superoesophageal, here præoesophageal) ganglion. The portion sending off the nerves of II. and III. is not, indeed, so distinct from the rest of the neural circle as in *Astacus*; but it holds the same relative position to the gullet. It is even within the bounds of fact to say that the origin of the nerves of IV. is nearer the fore than the hind part of that canal. Save at the price of making an arbitrary section, and imposing an illegal or unnatural boundary line, no one can contend against the Crustaceous nature of *Limulus* on the score of alleged suboesophageal origin of the antennal nerves, or those of the limbs (III, in the Plates of the present Memoir).

If Dr. Anton Dohrn be not prepared to pay this price, the analogies or resemblances indicated by Strauss-Dürkheim, Savigny, and Latreille, of *Limulus* to certain Arachnidans, will not suffice to outweigh the type of generative organs and extraneous impregnation, combined with the aquatic respiration and branchial organization of the present Condylipod and its palæozoic allies.

I fully concur with the estimable and experienced naturalist Van Beneden, that branchiæ of themselves may be an artificial class-character. But I cannot suppose that the incipient or larval relations of the nervous centres to the nerves are essentially different from those unquestionably demonstrable in the full-grown *Limulus*. The idea, therefore, of all the limbs succeeding the antennules (II) being supplied from the abdominal ganglionic cord, must be laid to the acknowledged difficulty which Anton Dohrn met with in tracing out their several relations in the embryo *Limulus* 2-3 lines in length†, transmitted to him preserved "in strong whiskey." Admitting, then, *Limulus* to be a

sein."—P. 638. [What Savigny has indicated and Strauss-Dürkheim has partially (one-sidedly) expressed, re-appears now under the light of the theory of evolution (descent)—that the connexion of Arachnids with Crustaceans is given by *Limulus* and the allied *Eurypteridæ*. *Limulus* is most nearly allied to the *Gigantostaca*; both appear to be allied to the Trilobites, although this affinity cannot be shown in all details. The morphologico-genealogical relations of these three families to the Crustacea cannot be stated at present, and will remain, perhaps, always dubious. At present we are entirely unable to say any thing of their relations to the Arachnida. Consequently only one course remains for us, viz. to form an independent group for these three families, with a common name, adopting that of *Gigantostaca* proposed by Hæckel, and to place it in the system at the side of the Crustacea.]

\* "Bei allen Krustern empfangen nämlich die beiden vorderen Extremitätenpaare ihre Nerven aus dem oberen Schlundganglion. Bei *Limulus* aber wird nur das vorderste Paar der Gliedmaassen von dem oberen Schlundganglion versorgt, die übrigen empfangen ihre Nerven aus der Bauchganglionkette."—A. DOHRN, *loc. cit.* p. 585.

† *Op. cit.* p. 586.



Crustacean (incipient, it may be), what are its nearest allies in that class? Do the grounds on which I reject a 'Trilobiten-Stadium' at any period of its larval life meet with any support from affinities manifested by the adult to other Crustaceous forms?

*Pterygotus* and *Eurypterus* resemble *Limulus* in the organs of vision, save that the facets of the large lateral compound eyes are less distinct or less conspicuous in the fossil, possibly exuvial, specimens of those extinct forms.

Both palæozoic genera manifest a clear and exclusive affinity to *Limulus* in the general proportions, modifications, and functions of the cephalotracheal limbs. In *Pterygotus* (fig. 14) the foremost pair is chelate, the hindmost pair lamellate, the intermediate pair are less differentiated and are alike. In *Slimonia* (fig. 15) the foremost pair is the smallest and shortest, the hindmost the longest, and it is also lamellate. In both genera all the cephalotracheal limbs, at least all but the foremost, had the basal joints beset with 'carding-spines,' showing their functional subserviency, as in *Limulus*, to the mouth as preparatory organs of digestion.

We may consequently infer, from the analogy of the food of the living King-crabs, that Nereids and other soft-bodied Annelids abounded in the sandy or muddy beds of the old ocean in which the Merostomata\* burrowed.

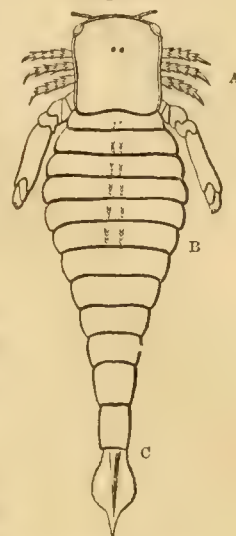
In these the cephalotracheal shield (figs. 13, 14, A) was small, both in breadth and length, as compared with that in *Limulus*, *Prestwichia* (fig. 17), and *Bellinurus*; but it was similarly shaped as regards the curved anterior trenchant fossorial margin. The mouth was inferior, bounded laterally by the carding-joints, and posteriorly by a 'labium,' or connate chilaria, of large size—and, if homologous with the parts in like relation to the mouth of *Limulus* (\* , \*, Plates II., II. A, III., & IV.), differing therefrom by the pair continuing the condition shown by the thoracetracheal limbs of *Limulus*. Whatever homology be adopted, the hindmost of the 'trophi,' or oral organs, is single and symmetrical in Eurypterids. No fossil Merostome has yet been discovered showing more than three pairs of cephalotracheal jaw-limbs between the foremost and hindmost pairs. Thus there is one pair less than in Xiphosures (fig. 8). In the fine fossil exuvium of the young *Pterygotus anglicus* figured by H. Woodward in his excellent 'Monograph on the Merostomata' (plate ii. fig. 1)†, there seem to be as many as five limbs on the left side, with spinigerous haunches; but it is uncertain whether the foremost of these may not be the fellow of the second, displaced from the right side. This, therefore, leaves the forcipate antennæ, or foremost pair of jointed cephalotracheal limbs, devoid, like that pair in *Limulus*, of the basal carding jaw-plate.

I think it of less moment to speculate as to which of the six pairs (II–VII) of cephalotracheal limbs in Xiphosures were undeveloped in Eurypterids, than to realize the certain correspondence of character of the five developed pairs in the latter family with those

\* This term signifies, and most aptly in its present adopted extent of application, the peculiar structure and function of the cephalotracheal limbs described in previous paragraphs.

† Vol. of the Palæontographical Society for 1866.

Fig. 15.



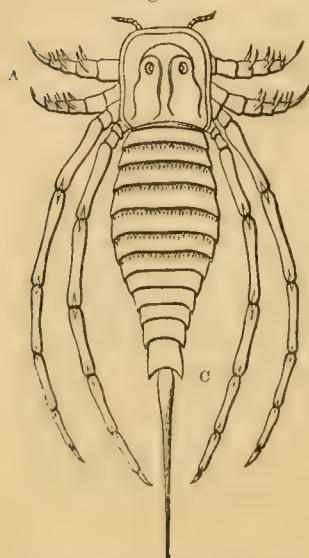
*Slimonia acuminata*, Wd.

attached to the Limuline cephaletron. As in *Limulus*, moreover, a partially coalesced pair of opercular plates extended backward in *Pterygotus* from the under and hinder border, more or less concealing the underparts of the two anterior segments of the thoracetron (fig. 14, B).

The foremost division of the body (A), in both *Slimonia* (fig. 15) and *Pterygotus*, is composed of fewer segments than in *Limulus*. The next division of the body, B, in Eurypterids, includes a greater number of segments; and the broadest of these but little exceed in that dimension the coalesced cephaletral segments. The pleonal ones, transitorily manifested at the basal part of the telson in *Limulus*, retain their individuality in Eurypterids, so that the distinction between thoracetron, B, and pleon, C, is arbitrary, and only the telsonic termination of the third division of the body is definable. Accordingly, the whole body of the extinct Merostomes is longer and narrower, exhibiting less of concentration and more of irrelative repetition, than in the existing Limuline form.

If shape and relative size affect so little the conclusion above supported of the homo-

Fig. 16.



*Styloneurus Loganii*, Wd.

logy of the cephaletron in Xiphosures and Eurypterids, much weight cannot be attached to the difference of form and proportions of the 'pleon' or 'telson' in the same question, especially with present knowledge of the intermediate modifications of this division of the body, as seen in *Eurypterus* (fig. 13)\* and *Styloneurus* (fig. 16). As the cephaletron of *Limulus* includes more segments and appendages than does that of *Pterygotus*, so likewise may the pleon of *Pterygotus* as compared with that of *Limulus*. The excess of segments of the thoracetron in Eurypterids (which excess H. Woodward is disposed to refer to another division of the body, which he terms 'abdomen') may be among those of which embryologists of *Limulus* believe themselves to have seen traces in its budding tail-spine. However that may be, or be accepted, the pleon or telson in all Merostomes is terminally pointed or spinous, and would help in the movements of the animal much in the same way as Lloyd and Lockyer have observed it to act in *Limulus*.

That this tail-spine (pleon and telson) is a serial homologue, reduced and simplified, of the segments, and not in the category of limbs or other mere appendages, the modifications thereof in some of the extinct allies and predecessors of *Limulus* give evidence of weight. The argument for its appendicular grade, from time, "that it is developed subsequently to the other segments," can only apply on the assumption or supposition that all true segments or 'somites' of a Crustacean are simultaneously developed. The statement that the 'tail-spine' is developed not only subsequently to, but "from the dorsal surface †" only of the body, has but the value of an unsupported assertion. If the attach-

\* Nieszkowski, "Der Eurypterus remipes aus den obersilurischen Schichten der Insel Oesel." Archiv. für die Naturkunde Liv- Ebst- u. Kurlands, Erste Serie, Bd. ii. tab. i. fig. 1"; quoted by Anton Dohrn, *loc. cit.* p. 640, Taf. xiv. fig. 21. H. Woodward, *Eurypterus brodiei*, from Pertou, 'Quarterly Journal of the Geological Society,' March 1871, p. 261, fig. 1.

† Prof. Huxley, in 'Medical Times and Gazette,' 1857.



ment of the budding pleon of a *Limulus* at the stage figured by Packard (pl. v. fig. 27, *op. cit.*) were so different in its vertical relation from that of the antecedent segment as to support the assertion as to the limited locality of its attachment, the legitimate inference would be that it represented a corresponding part of a body-segment. If successively developed axial divisions of the body-segments are only to be regarded as such when they happen to bear true appendages, many of the segments of the Merostomes, besides the terminal one, must be relegated to the category of 'peculiar' median appendages—a view which would much obscure and complicate the problem of determining the affinities of those primeval crustaceans on the basis of well-founded homologies.

Concurring with my colleague, Mr. H. Woodward, in the views of the affinities which are expressed by his extended application of Dana's term *Merostomata*, which thus becomes something more than a mere synonym of Gronovan's *Xiphosura*, I would remark, in reference to the relations, in time, of the latter to *Pterygotus*, *Eurypterus*, and allied extinct Silurian forms, that these manifest a more generalized character than do the *Xiphosures*. One cannot say that they are persistent or arrested embryonal forms or stages of development; for we have seen that *Limulus*, as soon as the germ-heaps are aggregated into unity or shape, assumes its concentrated character. Both families, together with the *Trilobitidæ*, exemplify that lower condition of the Crustacea which has been expressed by the term *Entomostraca*, in which, as Mr. Woodward has well remarked, the older, long and slender forms are analogous, in shape as well as in geological relations, to the macrurous *Malacostraca*, and the short and broad forms to the *Brachyura*. If we further indulged in suggesting that the *Merostomata* might be the ancestors of *Arachnida*, we might also conjecture that the Myriopods have come out of Trilobites; but this, at present, is not science. A superficial resemblance to the latter, as we have seen, is shown by the absence of the pleon in the earlier stages of the King-crab; but the very fact of the late appearance of this terminal division of the body, after all the segments, with their appendages, of the antecedent division ('thoracetron') have been formed, is decisive against any real or representative resemblance of the embryo *Limulus* to the Trilobites—on the acceptance, at least, of the original and valuable observations by Barrande\*, of the successive and later appearance of the abdominal ('thoracetræ') segments, in the space between the head ('cephaletron') and pygidium ('pleon'), in the embryos of *Sao hirsutus*, *Agnostus nudus*, and *Trinucleus ornatus* (fig. 12). These developmental phenomena bear a significant analogy to those observed by Newport† in the *Julidæ*—the successive appearance, viz., of body-segments, in the space (ib. B) anterior to the terminal or pygidial division (ib. C); such thoracetræ segments also appearing at successive moults, as in the Trilobites.

These, with other facts noted in the anatomical sections of the present paper, such as the fusion of the pair of cephalic ganglia, the shortness and thickness of the 'crura'

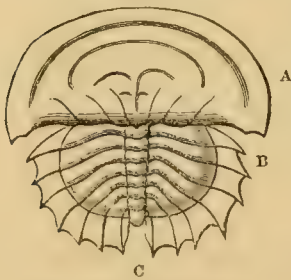
\* *Système Silurien du Centre de la Bohême*, 4to, 1852; section vii. pp. 257–276, "Métamorphoses et mode d'existence des Trilobites."

† "On the Organs of Reproduction and the Development of the Myriapoda," *Phil. Trans.* vol. cxxxi. 1841; and Owen, 'Lectures on Invertebrata,' 8vo, 1855, p. 394.

connecting these with the subœsophageal mass, in *Limulus*, giving the condition of that part of the nervous system, as in *Scorpio* and *Julus*, as an 'annular centre,' the nerve-supply in *Julus* of two pairs of jointed appendages from the superœsophageal lobes (Plate II, fig. 6), might be viewed in the following relation,—viz. that herein *Limulus* manifested the more 'generalized type' of articulate structure, in which not only Arachnidan but Myriapodal characters were associated with Crustaceous ones. But, in the development of *Limulus*, the pleon or tail-spine (=pygidium) was the last to appear, and, at its first budding, looked like a ninth segment of the thoracetron. Packard, as we have seen, speaks of indications therein (transitory, indeed) of segmentation of the crust; and such indications I have shown to be more strongly and lastingly given by the nervous system.

After formifaction and the attractive and repellant forces have produced, in the germ-mass, the phenomena of segmentation and vegetative repetition (as manifested in the similar and parallel heaps of granules, like bricks for the building), the inherited influences seem to overrule the polaric ones and operate in differentiating and adaptive lines, speedily showing the embryo-form of a *Limulus*; which, like that of *Astacus fluviatilis*, *Palæmon adspersus*, *Crangon maculosus*, *Eriphia spinifrons*, Spiders, and, one may add, Cephalopods, goes straight to the goal of parental characters. There is no divergence to a larval form enjoying for a term an active independent life. There is no metamorphosis, either naupliar, zoëal, or trilobitic.

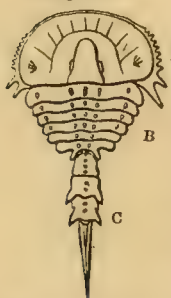
Fig. 17.

*Prestwichia rotundata.*

Other representative analogies, however, can be adduced, which are plain and intelligible. Arrest the development of *Limulus* at the tailless stage (figs. 7, 8), and one gets a '*Belinurus* or a *Prestwichia* stadium' (fig. 17). Stay awhile in serving the warrant, and you have the short-tailed palæozoic Limuloids—a '*Hemiaspis* stadium.'

Segments indicated by the nerve-pairs but concealed or suppressed by the crust at the base of the tail-spine in *Limulus*, were realized in *Hemiaspis limuloïdes* (H. Wd.). The progress from the general to the special, from vegetative repetition to concentrative unity, is exemplified in the living representative of the old Xiphosure (fig. 18) discovered by Salter in the

Fig. 18.

*Hemiaspis limuloïdes*, Wd.,  
*op. cit.*

bed of a Silurian sea now contributing to form the county of Shropshire. The ancestral pleon (c, ib.) has been almost "rubbed out" in the thousand-fold generations of which the Salem King-crab is the heir; but the palæozoic taint sticks to the nerve-element. Or shall we say that *Limulus*, made perfect for its sphere and habits of life, must have its "alpen-stock" unbroken, of compact stuff without joints near the grasped end? But then the teleologist or thaumatogenist has to give an account of the intermediate or 'evolutionary transitional' condition of the three pleonal segments manifest outwardly, as doubtless by their nerve-pairs and probably ganglion-centres within, but soldered together or "anchylosed," in König's and Baily's *Belinurus*, as in *Limulus*.

Should any persevere in objecting to the King-crabs' being called *Crustacea*, by



others the objection may be stronger to call them *Arachnida* or *Myriapoda*. Characters common to *Limulus*, with allied extinct gill-bearing, well-limbed *Articulata*, have not a class-value. I believe myself at one with the best Carcinologists in refusing to raise the *Merostomata* to an equivalency with *Crustacea*, *i. e.* to run them parallel with and alongside of the rest of the branchiated Condylapods. A class, after all, is an artificial group, a help to the classifier. One may call *Limulus* a Crustacean, and yet discern in its anatomy the evidence of its more generalized structure as compared with the *Malacostraca*. The merostomatous type preceded that of either the macrourous or brachyurous Crustacea; and in *Limulus*, the sole living representative, we have been able to detect characters subsequently overriding the crustaceous one, and intensified in the air-breathing members of the Apterous Insecta of Linnæus.

As compared with its longer-bodied and many-segmented predecessors, *Limulus* itself shows a concentrative specialization; but vegetative repetition still reigns in the limb-series. 'Internal antennules,' 'external antennæ,' 'mandibles,' 'maxillæ,' 'maxillipeds,' 'legs,'—all work together by their spinigerous haunch-joints in subserviency to mastication, and all terminate in chelæ. As compared with modern crabs, no structure is more striking and significant than the resistance, so to speak, of the heart in *Limulus* to the concentrative tendencies; it is still the dorsal vessel, though the body-part containing it has the breadth and shortness of the carapace of the crab, in which the heart is shaped to match. In both Merostome and Brachyure the neural axis supplying the cephalotral limbs is annular: but, in modern crabs, the subœsophageal part is defined by distance and by concomitantly elongated and slender, 'crura,' or connecting tracts between it and the superœsophageal or cerebral part. This differentiation had not taken place in *Belinurus*, *Neolimulus*, *Prestwichia*, and other palæozoic predecessors of Brachyura, whose organization we have to thank their longer-lived, lingering representative genus for enabling us to peer into.

That such glimpses, with concomitant tracing of the development of the individual *Limulus*, afford us some ground, and that the like work, with persevering quest of its palæozoic fossil allies, may afford more ground for at least guessing at the ways in which a preordained plan of derivation by congenital departures from parental form has operated in originating the various branches from a common ancestral articulate stem, is an encouraging faith.

That old Ocean should have afforded the chance conditions of origin of crustaceous subclasses, orders, genera, species, by 'Natural Selection,' is not conceivable by me: the metaphysical facts that there is 'will,' that a 'sense of the beautiful' exists, that 'a love of virtue' operates, opposes the supposition. Such facts suffice for the rejection of a 'Nature' working without will, taking no counsel of either the good or the beautiful, casting up from her dark abyss only eternal transformations of herself, furthering, with the same restless activity, decline and increase of organs, death and life of individuals, extinction and origination of species. Nevertheless I hold by the conviction that all forms and grades of *Articulata* are due to 'secondary cause or law' as strongly as

when I expressed the same belief in regard to the *Vertebrata*\*, and defined it as "the deep and pregnant principle in Philosophy"† evolved in the researches on the general homologies and archetype of the Vertebrate Skeleton.

The series of facts added to biology in the present century by these researches, with other correlated series, palæontological and embryological, of the kinds illustrated in the present memoir, render "thaumatogeny‡", or the hypothesis of direct creation of species, inadequate to their explanation. The invocation, by Cuvier, of successive miraculous interventions, creative and destructive, to solve or explain the phenomena of the succession of extinct species, chiefly made known by his grand discoveries, recalls the complexity of cycles and epicycles invoked to explain the facts of astronomy as they had accumulated in the time of Copernicus. He knew not how the twofold movements of the earth (rotation on its axis, revolution about the sun) were governed; but the hypothesis on those postulates simplified the comprehension and explanation of the phenomena of the heavens.

So the way of operation of "nomogeny," or the incoming of species by secondary cause, remains to be demonstrated; but its expository relation to the phenomena is a guarantee of its truth. Volition, with exercise and disuse of parts, invoked by Lamarck, are of the nature of "causæ veræ," but inadequate; premature births, congenital departures from parental characters, suggested by "Vestiges," meet some of the phenomena; "Natural Selection" suggests other conditions of "nomogeny."

Biology is in its Copernican stage. The analogy to Astronomy is close. The objection to the Canon of Frauenberg, that the rate of the whirl required by his hypothesis would send into space all things loose on the earth's surface, is akin to some of the cavils, as seemingly fatal, to the evolutionary view. The analogy of the course of physical science, and the accelerated rate of progress of those of life, since DeMaillet, Lamarck, and Oken, ceased to be exceptional advocates of Nomogeny, justify the expectation that this hypothesis will be developed into a known law, and one day receive its crowning demonstration from the Newton of Biology.

## § 12. DESCRIPTION OF THE PLATES.

### PLATE I.

#### *Limulus polyphemus.*

Fig. 1. Alimentary canal, hepatic ducts, part of the liver, and of the muscular system, *in situ*, viewed above, or from the dorsal aspect.

- A. Cephalotron: a'' its postlateral spinous production ('genal spine' of Trilobitology).
- B. Thoracetron.
- C. Base of pleon.

- i. Compound eye.
- a 1. Ocelli.
- h. Entapophysial pit of hindmost (by anchylosis) cephalotral segment.

\* On the Nature of Limbs, 8vo, 1849, p. 86.

† Ib. p. 10.

‡ Anatomy of Vertebrates, vol. iii. p. 814.



- i.* Intestine.
- i* 1-4. Entapophysial pits of thoracetron.
- k.* Terminal spine of the ocular or medilateral ridge of the carapace.
- l.* Anterior hepatic duct.
- m.* Posterior hepatic duct.
- m* 1-6. Marginal articulated spines of thoracetron.
- n* 1-7. Marginal spinous angles of thoracetransal segments.
- n.* Liver.
- n''.* Hepatic lobe, partially injected from the duct.
- o.* Dilated beginning of intestine.
- s.* Stomach.
- t, t.* Fasciculi of 'depressores thoracetri' muscles.

Fig. 2. Heart and vessels, with parts of ovaria, *in situ*, viewed from above.

- A, B, C,* as in fig. 1.
- a.* Heart.
- b.* Part of pericardial sinus.
- b'.* Part of pericardial sinus laid open.
- c, c.* Ostia venosa.
- e, e.* Neural arteries.
- f, f'.* Epimeral arteries of cephalotron.
- g, g'.* Epimeral arteries of thoracetron.
- h.* Ocellar artery.
- i* 1-6. Entapophysial pits of thoracetron.
- n.* Medilateral vein and sinus of cephalotron.
- o.* Oviduct.
- p.* Anterior thoracetransal vein.
- q.* Middle thoracetransal vein.
- r.* Posterior thoracetransal vein.
- s.* Median thoracetransal vein.
- u, u.* Fasciculi of the 'levator telsoni.'

## PLATE II.

### *Limulus polyphemus.*

- Fig. 1. Longitudinal section, with side view of the nervous system, the heart laid open, and the alimentary canal *in situ*. The explanation of the parts is given in the outline of this figure in Plate II A.
2. Longitudinal section of cephalotron and fore part of the alimentary canal, showing the relations to the mouth of the cephalotransal limbs. The explanation of the parts is given in the outline of this figure in Plate II A, which also includes figures 3, 4, 5.
  6. Anterior view of the head of *Julus terrestris*, dissected to show the cephalic or supercæsoophageal lobes, and the nerves to the eyes, antennæ, and mandibles (magn. 6 diameters).
  7. Upper view of the brain and nerves, with the beginning of the ventro-chordal part of the neural axis of *Julus terrestris* (magn. 6 diameters).
  8. Upper view of the cephalic lobes, with the optic nerves and disposition of the beginning of the stomato-gastric system of nerves upon the corresponding part of the alimentary canal of *Julus terrestris* (magn. 6 diameters).

## PLATE II A.

### *Limulus polyphemus.*

Fig. 1. Outline of figure 1, Plate II., giving a side view of heart, alimentary canal, and nervous system.

- A, B, C, I & a I,* as in Pl. I.
- A'.* Under or vaulted surface of cephalotron.
- B''.* Anal segment of thoracetron.
- II.* Antennula.
- III.* Antenna.
- IV.* Mandibula.
- V.* Præmaxilla.
- VI.* Maxilla.

- vii. Maxilliped.
- \* Chilarion.
- viii. Lid-plate.
- ix. First gill-plate.
- x. Second gill-plate.
- xi. Third gill-plate.
- xii. Fourth gill-plate.
- xiii. Fifth gill-plate.
- b. Dorsal wall of cephalotron.
- c. Ventral wall of cephalotron.
- d. Digging-border of cephalotron.
- e. Holding-border of cephalotron.
- g. Entering process of thoracetron.
- h. Entosternon.
- i. Intestine.
- m 1. Levatores thoracetri.
- m 7. Levatores telsi.
- m 8. Obliqui telsi.
- m 9. Depressores telsi.
- n a. Ocellar nerve.
- n A. Ocular nerve.
- n II. Antennular nerve.
- n III. Antennal nerve.
- n IV. Mandibular nerve.
- n v. Premaxillary nerve.

- n vi. Maxillary nerve.
- n vii. Maxillipedal nerve.
- n viii. Opercular nerve.
- n \*. Chilarian nerve.
- n ix-xiii. Nerves to branchigerous limbs.
- n xiv. Nerve of anal segment.
- o. Ostia venosa.
- pl. Pleonic plexus.
- r. Muscular wall of heart.
- s. Neural artery.
- t. Pleonic artery.
- a. Brain, or superæsoophageal nervous centre.
- β. Neural ring.
- γ. Neural cords.
- δ. First ganglion.
- ε. Second ganglion.
- ξ. Third ganglion.
- η. Fourth ganglion.
- θ. Fifth or terminal ganglion.
- χ. Ganglionic loop.
- λ. Pleonal nerve, or continuation of neural cord.
- μ. Principal nerve of
- pl. Pleonal plexus.
- a 1-4. Dorsal nerves of four anterior coalesced pleonal segments.

Fig. 2. Outline of figure 2, Plate II, giving a vertical longitudinal section of fore part of cephalotron and alimentary canal, with the cephalotral limbs or appendages of the left side. (The Preparation is No. 477 a, in the Physiological Series of the Museum of the Royal College of Surgeons: 'Descriptive and Illustrated Catalogue,' 2nd ed. 8vo, 1852, p. 132.)

- A, II to VII, and \*, as in figure 1.
- b. Dorsal wall of cephalotron.
- c. Ventral wall of cephalotron.
- d. Digging-border.
- f. Chitine.
- g. Pigment-layer.
- æ. Œsophagus.
- h. Entosternon.
- i. Intestine.
- l. Anterior hepatic duct.

- m. Posterior hepatic duct.
- p. p. Carding-plates, or palpi, of haunch-joints of III-VII.
- \*. Chilarion, a seemingly serial repetition of haunch-joints.
- q. Median lobe of ovary.
- r. Proventricular or cardiac part of stomach.
- s. Gizzard.
- mt. Pyloric prominence.

Fig. 3. Outline of the maxilla (6th cephalotral limb).

- 1. Coxa.
- p. Its "palp," or carding-plate.
- 2. Basis.
- 3. Merion.

- 4. Cnemion.
- 5. Propes.
- 6. Dactylus.



Fig. 4. Outline of maxilliped (7th cephaletal limb).

- |                         |                              |
|-------------------------|------------------------------|
| 1-5, as in fig. 3.      | <i>r.</i> Flagellum.         |
| 6. Lamelligerous joint. | <i>s.</i> Cnemial appendage. |
| 7. Chelate extremity.   | <i>t.</i> Terminal lamellæ.  |

Fig. 5. Mandibula (4th cephaletal limb) dissected for the muscles.

- |                                     |                                  |
|-------------------------------------|----------------------------------|
| <i>a.</i> Extensor basis mandibulæ. | <i>e.</i> Propedal entapophysis. |
| <i>b.</i> Flexor basis.             | <i>f.</i> Flexor propedis.       |
| <i>c.</i> Merional entapophysis.    | <i>g.</i> Flexor dactyli.        |
| <i>d.</i> Flexor merioni cnemiique. |                                  |

## PLATE III.

*Limulus polyphemus.*

Right half of the male King-crab, with the nervous system dissected from the ventral surface. The explanation of the parts in this figure is given in the outline copy in Plate IV.

## PLATE IV.

Fig. 1. Outline of figure 1 in Plate III., showing the nervous system, from the lower or ventral aspect.

- |                                                                                      |                                                   |
|--------------------------------------------------------------------------------------|---------------------------------------------------|
| <i>A'</i> . Inferior concave surface of cephaletron.                                 | <i>n xv.</i> Nerve of anal segment.               |
| <i>B'</i> . Infero-lateral surface; <i>B''</i> Infero-median surface of thoracetron. | (The other letters and figures as in Plate II A.) |

Fig. 2. Compound eye and terminations of ocular nerve, from the dorsal aspect: magnified 6 diameters (*Limulus polyphemus*).

- |                                                        |                                                         |
|--------------------------------------------------------|---------------------------------------------------------|
| <i>d.</i> Dorsal branch and divisions of ocular nerve. | <i>v.</i> Ventral branch and divisions of ocular nerve. |
|--------------------------------------------------------|---------------------------------------------------------|

Fig. 3. Compound eye of a Trilobite (*Phacops conophthalmus*): magnified 3 diameters.

Fig. 4. Portion of the same compound eye: magnified 10 diameters.

Fig. 5. Entosternon and attached parts of muscles. (After Van der Hoeven, *op. cit.*).Fig. 6. Chief parts of ovarium, oviducts, and opercular plate, from the upper or inner surface (*Limulus polyphemus*).

- |                                                 |                                                   |
|-------------------------------------------------|---------------------------------------------------|
| <i>m''</i> . Muscles of operculum.              | <i>q**</i> . Postero-lateral cephaletal branches. |
| <i>o, o.</i> Oviducts.                          | <i>r.</i> Articular surface of opercular plate.   |
| <i>p.</i> Oviducal outlets.                     | 2. Second joint of opercular plate.               |
| <i>q.</i> Postero-median lobe of ovary.         | 3. Third joint of opercular plate.                |
| <i>q*</i> . Antero-median lobe of ovary.        | 4. Appendages of opercular plate.                 |
| <i>q''</i> . Antero-lateral loops and branches. |                                                   |

Fig. 7. Section of terminal part of oviducts. (After Van der Hoeven, *op. cit.*)

- a.* Oviduct; *b.* anterior labium; *c.* portion of opercular plate.

Fig. 8. Portion of opercular plate with terminations of the sperm-ducts, *p.* (After Van der Hoeven, *op. cit.*)

## PLATE V.

*Limulus polyphemus.*

Fig. 1. Nervous system, from the upper or dorsal aspect.

- |                                  |                           |
|----------------------------------|---------------------------|
| <i>a.</i> Superæsoophageal mass. | <i>b.</i> Œsophageal ring |
|----------------------------------|---------------------------|

- |                                   |                                   |
|-----------------------------------|-----------------------------------|
| <i>n a.</i> Ocellar nerve.        | <i>n 11.</i> 7th Epimeral nerve.  |
| <i>n 1.</i> Ocular nerve.         | <i>n 12.</i> 8th Epimeral nerve.  |
| <i>n 3.</i> Gastric nerve.        | <i>n 13.</i> 9th Epimeral nerve.  |
| <i>n 4.</i> 1st Epimeral nerve.   | <i>n 14.</i> 10th Epimeral nerve. |
| <i>n 5.</i> 2nd Epimeral nerve.   | <i>n 15.</i> 11th Epimeral nerve. |
| <i>n 6.</i> Its recurrent branch. | <i>n 16.</i> 12th Epimeral nerve. |
| <i>n 7.</i> 3rd Epimeral nerve.   | <i>n 17.</i> 13th Epimeral nerve. |
| <i>n 8.</i> 4th Epimeral nerve.   | <i>n 18.</i> 14th Epimeral nerve. |
| <i>n 9.</i> 5th Epimeral nerve.   | <i>n 19.</i> 15th Epimeral nerve. |
| <i>n 10.</i> 6th Epimeral nerve.  | <i>pl.</i> Pleonal plexus.        |

(The preparation is No. 1303 c, in the Physiological Series of the Museum of the Royal College of Surgeons.)

Fig. 2. Left gill-limb, with attached branchia.

*a.* Tract of efferent branchial vessels.

Fig. 3. Branchial lamella; *a*, efferent plexus.

All the figures, save where otherwise stated, are of the natural size.

#### WOODCUTS.

Fig. 1. Cell-egg, with yolk-cells developing: magnified 130 diameters (*Limulus polyphemus*).

Fig. 2. Impregnated egg after disappearance of primitive cells: magnified 30 diameters: id.

Fig. 3. Section of egg-coat and germ-trace: magnified 130 diameters: id.

Fig. 4. Ovum with embryo-trace: magnified 10 diameters: id.

Fig. 5. Ovum with embryo further developed, side view: magnified 10 diameters: id.

Fig. 6. Ovum with embryo, under-view: magnified 10 diameters: id.

Fig. 7. Embryo *Limulus*, just before hatching, back view: magnified 13 diameters.

Fig. 8. Newly hatched *Limulus*, under-view: magnified 9 diameters.

Fig. 9. *Nauplius*, or young of *Apus cancriformis*: magnified.

Fig. 10. *Nauplius*, or young of *Cyclops quadricornis*: magnified.

Fig. 11. Zoea, or larva of *Penæus*.

Fig. 12. Five stages of the development of a Trilobite (*Trinucleus ornatus*, Stb.), selected from the more numerous series in Barrande's 'Système Silurien du Centre de la Bohême,' 4to, 1852, pl. 30.

*a.* Larva consisting of the cephalotroch, and pleon *c*: *b.* Larva showing the characteristic elongation of the posterior angles of the cephalotroch, or "genal spines:" *c.* Larva with one thoracotroch segment *b*: *d.* Larva with two thoracotroch segments *b*; *e.* Young animal showing mature number of six thoracotroch segments *b*, and fully lengthened "genal spines."

Fig. 13. *Eurypterus Scouleri*, Hbt.; reduced restoration (Carboniferous Limestone).

Fig. 14. *Pterygotus anglicus*, Ag.; reduced restoration (Devonian of Farfarshire).

Fig. 15. *Slimonia acuminata*, H. Wd.; reduced restoration (Upper Silurian).

Fig. 16. *Styloneurus Logani*, H. Wd.; reduced restoration (Upper Silurian).

Fig. 17. *Prestwichia rotundata*, H. Wd.; two-thirds nat. size (Coal-measures).

Fig. 18. *Hemiaspis limuloides*, H. Wd.; two-thirds nat. size (Lower Ludlow).

(The figures 12-18 are copied from those reproduced by H. Woodward, in his excellent paper "On the relationship of the Xiphosura to the Euryptera and to the Trilobita and Arachnida" in the 'Popular Science Review' for October 1872.)



Fig. 1.

Fig. 2.

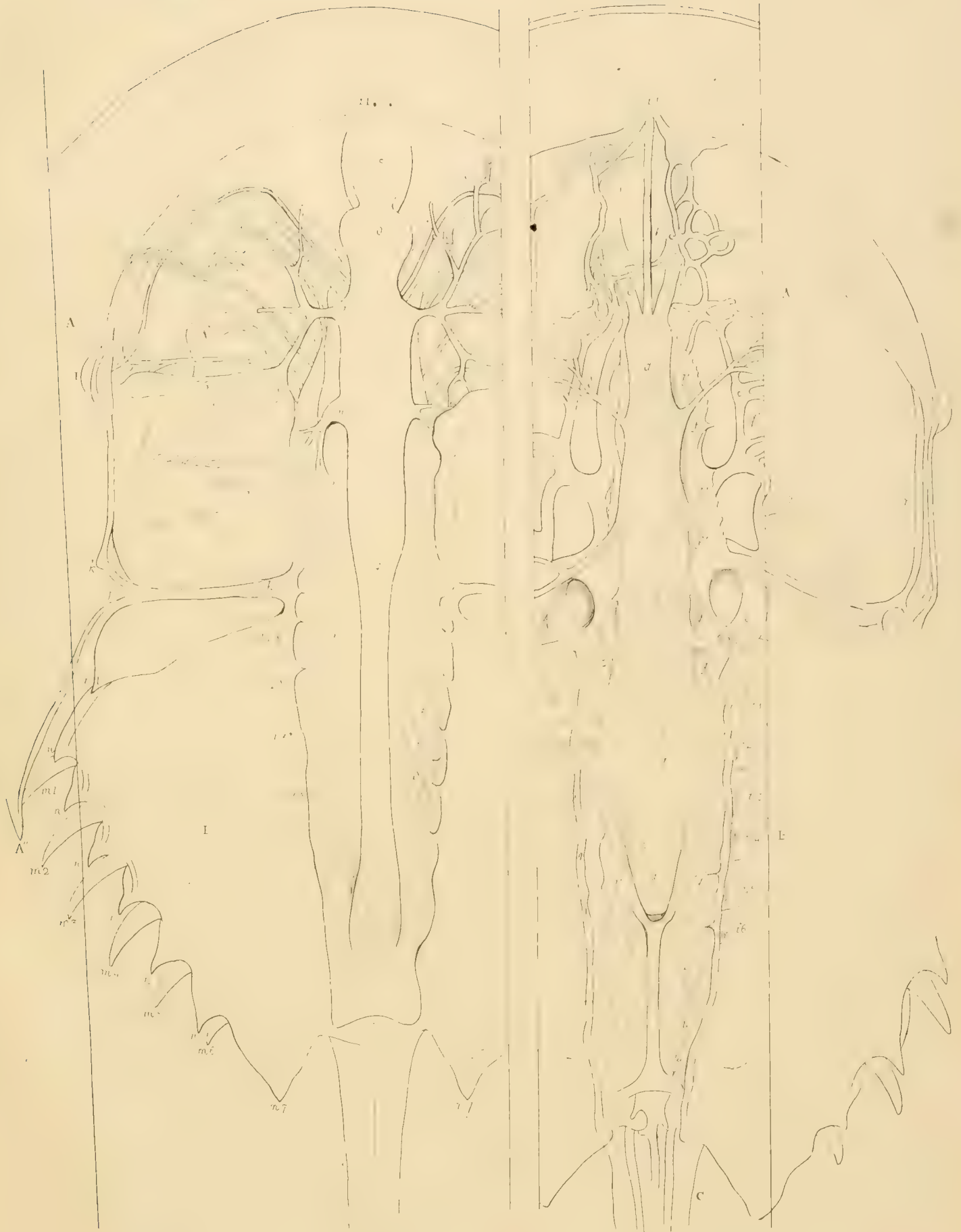












Plate II<sup>A</sup>













Fig 1



Fig 2



Fig 3

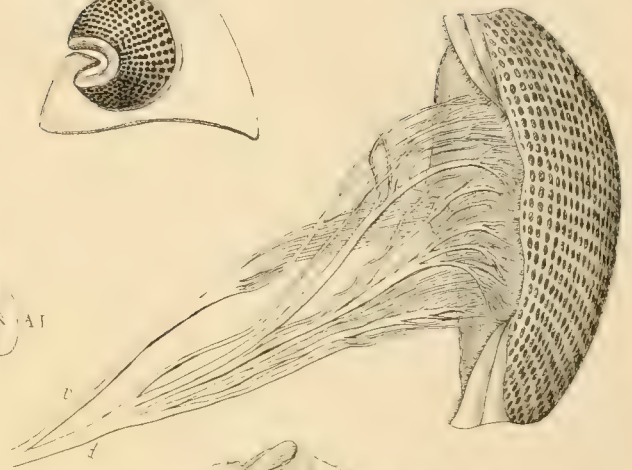


Fig 4

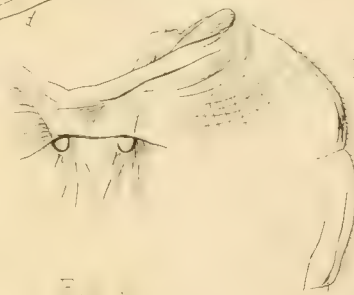


Fig 5

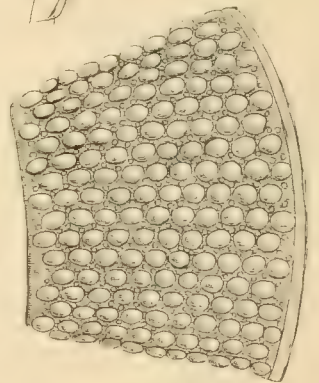


Fig 6

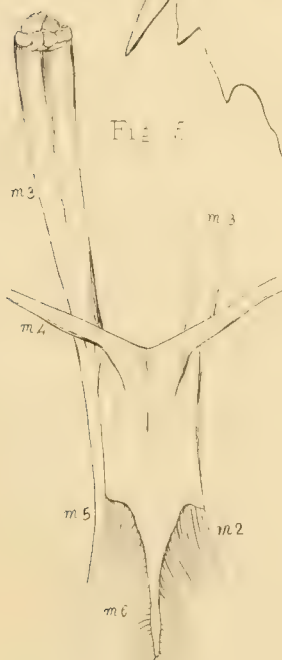


Fig 7



















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